

THE REPRESENTATION OF THE VISUAL
FIELD ON THE SUB-CORTICAL CENTERS
OF THE CAT AND RABBIT.

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by

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I. INTRODUCTION

1. Preamble.

As far back in the human past as there is a record the supreme importance of vision and of its instrument, the eye, has been recognized. The obtrusive reality and indispensability of the subjective phenomena of vision and the manifest connections of sight with its structural attributes have always had a vivid appeal to a host of philosophic and scientific minds. Until the 18th Century interest in the visual pathway was almost wholly confined to the infranuclear division and with the general advancement of knowledge this interest began to spread to the cerebral cortex and subsequently to the sub-cortical centers. Seeking correlation between structure and function, the questions raised by von Haller 1769 concerned the very foundations of knowledge of the nervous system, and stirred in the wake of his work controversy, as confused as acrimonious. Of this phase, Polyak 1955 writes, "plainly supernaturalism and transcendentalism, even among the scientific workers of that period, were still too strong to permit of an unbiassed study of the brain with the same scientific approach as that used for the investigation of less sacred parts of the human anatomy...", and

Lashley 1929, "it is difficult to discover the truth in this record of contradiction". The difficulty of even the straightforward anatomical problem is indicated by the fact that it took over three generations of diligent effort to reveal the relationships of the lateral geniculate nucleus and the visual cortex to the process of vision. Polyak 1955, reviewing the voluminous literature of this period, attributes to Munk 1879, 1881, the earliest experimental contribution to the theory of orderly retinal projection. Munk, in pursuance of Weber's, Graefe's and Meynert's ideas of topographical representation, made experimental lesions of the cerebral cortex of dogs and monkeys. From his experiments, he mistakenly concluded that the temporal portion of the retina was represented in the lateral portion of the ipsilateral "visual area" and the much larger nasal portion of the retina in the larger medial part of the contralateral visual area. Sharpey-Schaefer 1888, 1889, made experimental observations on the organization of occulo-motor centers in the cortex of the occipital lobes and postulated a similar organization of the adjacent sensory visual area. Willbrand 1890, observing scotomas of central origin, concluded that the two homonymous retinal halves were represented in a common cortical area instead of independently, side by side, as Munk had

earlier insisted. Of this, Willbrand postulated a hypothesis according to which the two sets of optic nerve fibers, arriving from conjugate points in the homonymous halves of the two retinae, come to lie very close together in the optic pathway, each terminating in a minute territory of the cortex adjacent to its fellow; hence conceiving the cortex as a mosaic of such double units. The most prominent and controversial name of this phase is that of Henschen 1893; during his activity, spreading over almost half a century, he investigated all parts of the visual pathway, the optic nerves, sub-cortical centers, visual radiations and the cortical centers, in brain specimens in which various types of field defects had been observed during life and became convinced of the stable projection of the retina on to the subsequent links of the pathway and cortex. Commenting on his work, Polyak 1955 writes, "It is fair to say that, even though he was unable to avoid all the pitfalls, progress in the knowledge of the visual system, achieved during the subsequent years, was in no small degree the result of his labours and interest".

With the advent of the 20th Century the guess-work and speculation, characteristic of much clinical thinking of the preceding decades, with its "self bestowed freedom to create plausible hypo-

theses of anatomical structure, to explain away difficult diagnostic situations" became gradually recognized as unsatisfactory. Clearly, only evidence which could be observed and verified was acceptable as a criterion fit for the solution of problems. Foremost among the new methods was the development of refined histological techniques and especially of the Marchi method of staining degenerating myelinated axons; the use of this by many distinguished workers resulting in the accumulation of sufficient anatomical evidence to establish with certainty the existence of a spatial orderliness in the projection of sensory surfaces upon the higher centers of the nervous system.

In the visual system the primary problem has been the identification of the visual pathway - the fiber systems along which the impulses arising in the eyes pass to the various subcortical levels and finally to the cortex - their precise localization, boundaries, and the extent of the terminal areas of the pathway. The second problem has been to determine whether, and to what extent, the original spatial and dimensional relationships present in visual space and in the retina are preserved in the pathways and centers, and if they are, how and where the various distinct areas of the retina, i.e. the fovea, the extra-foveal peripheral quadrants, the

horizontal and vertical meridians, were represented in the various levels of the visual pathway.

2. Histological Studies of the projection of the retina on the visual pathway.

The subcortical distribution of the visual pathway in vertebrates has been extensively studied. For the opossum - Tsai 1925, Bodian 1937; ferret - Jefferson 1940; phalanger - Packer 1941; rabbit - Pavlov 1900, Loepp 1912, Minkowski 1920, Brouwer and Zeeman 1925, 1926, Jefferson 1940; rat - Lashley 1937, Hayhow, Sefton and Webb 1962; sheep - Nichterlein and Goldby 1944; goat - Minkowski 1920; cat - Probst 1900, Minkowski 1920, Barris and Ingram 1934, Barris, Ingram and Ranson 1935, O'Leary 1940, Hayhow 1958; dog - Probst 1900, Rioch 1929; monkey - Minkowski 1920, Brouwer and Zeeman 1925, 1926, LeGros Clark and Penman 1934, Crosby and Henderson 1948.

These workers, enucleating one eye, traced the degenerating axons by the Marchi method. Apart from revealing gross details of the distribution of the subcortical pathway and the extent of fiber decussation in the chiasma, the Marchi method, after enucleation of an eye, fails to reveal evidence of topographical localization.

The transneuronal atrophy in the optic tract distribution, resulting from small retinal lesions, have been studied by Marchi degeneration methods. In the teleost fish *Leuciscus rutilus* by Lubsen 1921, in another teleost *Salmo irideus* - Akert 1949; rabbit - Brouwer and Zeeman 1925, 1926, Overbosch 1927; cat - Overbosch 1927; monkey - Minkowski 1913, 1920, Brouwer and Zeeman 1925, Clark and Penman 1934, Hoyt and Luis 1962.

In twelve experiments, Brouwer and Zeeman made localized lesions in the retinae of rabbits under ophthalmoscopic observation and traced the resulting degeneration through the optic nerve and tract to the lateral geniculate nucleus and superior colliculus, and succeeded in demonstrating a consistent topographical projection of the retinal quadrants. In the dorsal nucleus of the geniculate they found the temporal half of the retina projecting to the mesial aspect of the nucleus, the nasal retinal half to the lateral aspect, the upper half of the retina to the lower half of the nucleus, and the lower retinal half to the upper half of the nucleus.

Overbosch 1927, quoted by Brouwer 1927, confirmed the findings of Brouwer and Zeeman in the rabbit geniculate and colliculus, he too failing to observe any uncrossed fibers reaching the colliculus. In the cat, he observed a similar quadran-

tic projection on the dorsal geniculate nucleus, the upper retinal half projecting anteriorly, the lower retinal half dorsally, the nasal half retina on the lateral aspect of the nucleus, and the temporal hemi-retina on the medial aspect of the nucleus.

Although this method allows of the recognition of quadrants of projection, it is not sufficiently precise to provide evidence of a "point to point" projection, for the dispersal of Marchi granules is usually so extensive that it has not been possible to discriminate between small retinal lesions less than 30° - 40° apart. The inherent limitations of the method have been due to several factors:-

1. Retinal lesions always interrupt fibers of passage coming from the retina peripheral to the lesion.
2. The possibility that there may be two systems of retino-collicular fibers, the thicker fibers forming a diffuse projection while the thinner fibers form the retino-topically organized projection. Herrick 1941 found this to occur in *Amblystoma*, and Chang 1952 has suggested that the same may be true of mammals. If so, the Marchi technique

by selective staining of the thicker fibers may mask the organized projection of the thinner.

3. Fibers from the peripheral retina may form the primary retino-collicular system whose spatial organization is coarser than that of the macular fibers which relay in the geniculate nucleus, Whitteridge 1960.

4. There may exist a selective distribution of small fibers to the colliculus and larger fibers to some laminae of the dorsal lateral geniculate nucleus of the cat, O'Leary 1940, Bishop and Clare 1955.

5. The absence of myelin on the terminal arborizations of a fiber make it impossible to draw a rigid distinction between degenerating fibers of passage and the more haphazardly orientated terminal or preterminal fibers, within an area defined by their presence, as a site of terminal degeneration, Beresford 1961.

The retrograde degeneration occurring in the subcortical centers, following experimental lesions of the visual cortex, have been studied by several.

Putnam and Putnam 1926 quote Von Monakow 1881 as being the earliest to use this technique to study geniculo-cortical connections. Making experimental lesions of the striate cortex of rabbits, he observed the resulting degeneration of the lateral geniculate nucleus, though no precise information as to topography was elicited. Von Monakow 1883, 1885 found that in the cat the medial portion of the visual cortex projected laterally on the dorsal geniculate nucleus, the lateral part of the visual cortex medio-frontally on the geniculate, and the posterior part of the cortex postero-laterally on the geniculate.

Van Valkenburg 1911, quoted by Putnam and Putnam, observed that small lesions of the striate cortex produced circumscribed areas of degeneration in the cat's dorsal geniculate nucleus, but made no investigation into the pattern of projection.

Minkowski 1913 made experimental lesions in the striate cortex of cats, dogs and monkeys. In his series of five cats, he made lesions 0.5 cms. in diameter in the striate cortex and demonstrated consistent degeneration in localized regions of the lateral geniculate nucleus, revealing the pattern of topographical organization between the geniculate and the visual cortex. He found the anterior and superior part of the visual cortex

related to the anterior and inferior part of the geniculate, the posterior and inferior part of the cortex with the posterior and superior geniculate, whereas the medial and lateral extents of the visual cortex had no well defined areas of projection on the geniculate.

Polyak 1927, studying the degeneration resulting from small striate lesions, observed that the fibers of the optic radiation showed a definite arrangement of its fiber bundles, a pattern maintained therein until the fibers reached the cortex. The cortical field was well delimited, with no diffuse distribution of fibers in the occipitoparietal lobe. The caudal half of the cortical field in the gyrus lateralis posterior corresponded with the "area striata" of Cajal and Brodmann's Area 17, yet overlapping laterally, the adjacent cortical zone along the postero lateral sulcus being situated in the lateral lip of the lateral convolution and in the medial lip of the suprasylvian convolution; this area of cortex, corresponding in part, or entirety, with Brodmann's Area 18-19 and the peri-parastriate cortex of Eliot Smith, Polyak noting however that the fibers reaching the extra-striate cortex showed some differences, in number and caliber, from those fibers reaching the striate cortex. These cortical lesions, being extensive, did not reveal the

topographical relationships between cortex and geniculate.

Putnam and Putnam 1926, studying the effects of localized cortical lesions in rabbits, produced evidence of a fixed and definite anatomic projection on the lateral geniculate, the size of lesion in one being proportional to the size of lesion in the other in the areas devoted to monocular vision; striate lesions, however, producing no demonstrable degeneration in the superior colliculi of either side or in the pars ventralis of the geniculate nucleus. Combining their observations of the geniculo-cortical relationships with those obtained by Brouwer and Zeeman 1925 with respect to the retino-geniculate projections, they deduced the pattern of retino-cortical projection topography; the nasal retinal quadrants projecting to the posterior inferior cortex, the temporal retina to the anterior superior cortex, the superior retinal quadrants to the superior aspect of the cortex, the inferior retina being projected to the inferior aspect of the cortex; binocular vision being mediated in a relatively large cortical area anterior to the area, receiving the projection from the temporal quadrants of the retina.

Marshall, Talbot and Ades 1943, making small lesions of the striate cortex in cats, observed

the retrograde degeneration in areas of the geniculate nucleus consistent with the pattern described by Minkowski, yet in contradistinction to Polyak 1927, reported that they could not obtain unequivocal evidence of geniculate degeneration following lesions of the suprasylvian gyrus.

The technique of establishing patterns of cellular connections by retrograde degeneration, though beset with the customary difficulties of the Marchi method, has revealed gross evidence of a quadrantic projection of the retina on the cortex; yet it may be unwise to infer, solely on this basis, that it is exclusively so, for the specific factor determining which, or how many, of a number of cellular extensions need be cut before the cell degenerates is as yet unknown. Doty 1961 writes, "It is thus premature to assume that the disappearance of a geniculate cell, following section of an unknown number of its collaterals, signifies that it sent collaterals only to the restricted locus of injury. The cell might well send collaterals into widely separated cortical areas and readily survive their separate loss, yet degenerate upon removal of a more compact group of branches".

Electrode on the surface of the superior colliculus of the cat, using as a stimulus a spot of light subtending 4.2° in the field.

3. Electrophysiological Studies of the projection of the retina on the visual pathways.

(i) Representation on the sub-cortical centers.

Talbot and Marshall 1941 introduced the technique of mapping the representation of the visual field by recording, from the visual cortex, the action potentials evoked in response to a small light in the visual field. Their method was used by Apter 1945 to map the projection of the visual fields on the superior colliculus of the cat; the optic tectum of the frog by Gaze 1958, Gaze and Jacobsen 1959, Jacobsen 1962; the optic tectum of the pigeon Hamdi and Whitteridge 1953; the colliculus of the goat Cooper, Daniel and Whitteridge 1953; and the colliculus of the rabbit Hamdi and Whitteridge 1953. Buser and Dusardier, 1953, stimulating the retina with bipolar electrodes 1 mm. apart, recorded evoked potentials in the contralateral tectum of the cat-fish, tench and carp, but the relatively small size of the fish eye, with its poor visual capacity, and the inadequacy of their technique enabled them to demonstrate only a quadrantic pattern of projection.

Apter 1945 recorded the action potentials with a moist wick electrode on the surface of the superior colliculus of the cat, using as a stimulus a spot of light subtending 4.2° in the field.

Finding that, for any position of the electrode, the evoked response was of minimal latency and maximal amplitude only when the stimulus occupied a strictly defined and determined locus in the visual field, she was able to map the projection in some detail. The vertical meridian splits the field such that the nasal half field is represented on the contralateral colliculus, the temporal half ipsilaterally, the vertical meridian being projected along the rostral margin of the colliculus, with the horizontal meridian running rostro-caudally, and slightly obliquely, across its summit. On each collicular surface the representation of the ipsilateral temporal half field and of the contralateral nasal half field were superimposed in such a manner that corresponding points in the homonymous half fields were in register.

Although Apter's data give some indication of a relatively larger area of representation for the central field and that the horizontal and vertical meridians undergo unequal distortion when projected on the collicular surface, the evidence obtained by recording evoked surface waves is necessarily inadequate to allow of a quantitative expression of these features. Hamdi 1953, Hamdi and Whitteridge 1953, Cooper, Daniel and Whitteridge 1953, studying the projection of the visual

fields on the tectum of the pigeon and colliculus of rabbit and goat, used small steel needle electrodes to record the responses evoked by a neon flash subtending 0.5° in the visual field. Although they established the projection of the meridians on the tectal and collicular surfaces, the paucity of observations in any single experiment made the details of projection of the area centralis uncertain.

Gaze 1958, using the evoked potential technique and recording from tungsten micro electrodes, demonstrated a point to point projection of the visual fields on the optic tectum of the frog. His method of electrode placement, in one or two rows across the tectum, was however inadequate to provide evidence of a representation of the area centralis retinae which had been described by Chievitz 1889.

Jacobsen 1962, extending this work, mapped the available surface of the tectum, placing his electrode on the tectum on an equally spaced grid 200 microns apart. The greatly increased precision of this method enabled him to demonstrate the presence, on the tectum, of a central area of increased resolution and to show that the vertical and horizontal co-ordinates of the field and retina undergo a geometrical transformation in the course

of their projection to the tectum. The distortion along the vertical meridians being greater, the concentric "circles" of latitude in the field become projected on the tectum, in an ellipsoid fashion. Expressing this relationship quantitatively, he finds the variation of the "magnification factor" (i.e. linear extent of visual surface concerned with the representation of 1° of the visual field - Daniel and Whitteridge 1961) along the horizontal and vertical meridians significantly different. Ganglion cell counts were made along the meridians of the retina, and the variation of these counts with retinal eccentricity away from fixation point show a close correlation with that of the corresponding magnification factor curves. These findings lead Jacobsen to comment "that the results lead one to believe that the geometrical properties of visual space have their analogies in the geometrical organization of the visual system". Proof of this, however, would yet depend on a much more precise knowledge of the patterns of interconnection of the retinal units, the details of distribution of afferent visual fibers in the nervous system, ~~and~~ the patterns of their terminal arborizations and connections, than is, as yet, available.

antero-lateral area Visual II, the evoked responses

(ii) Representation on the cortical centers.

A. Rabbit.

Talbot, Woolsey, Thompson 1946; Thompson, Woolsey and Talbot 1950. Using as a stimulus a flash subtending 4° at the eye, these workers determined the retinal representation on the exposed surface of the rabbit's cortex, leading off the flash evoked responses with a moist cotton wick electrode. The limits of the visual area, obtained by contralateral photic stimulation, agreed well with those obtained by O'Leary and Bishop 1937, 1938 by electrical stimulation of the contralateral optic nerve - the visual responsive area - including the area occipitalis as well as the adjacent area peristriata; being disposed on the cortex in the form of a band extending diagonally from the antero-medial to the postero-lateral portion of the hemisphere. They determined the vertical meridian for binocular vision to be situated 20° from the sagittal plane of the visual field, and when projected on the cortex, to divide the binocular area into approximately equal halves. The visual area lying antero-lateral to this line shows a pattern resembling a mirror image of the area which lies postero-medial to the line. The slightly larger postero-medial area was designated Visual I, the smaller antero-lateral area Visual II, the evoked responses

from both being very similar in form, latency and amplitude.

These results differ considerably from those deduced by Putnam and Putnam 1926 on the basis of their studies of retrograde degeneration, and Brouwer's 1925 studies of degeneration in the geniculate following retinal lesions.

Thompson, Woolsey and Talbot placed their 90° vertical meridian on the cortex, very nearly at right angles to the dividing line between the nasal and temporal fields, as reported by Putnam and Putnam, the horizontal meridian likewise being at right angles to that of Putnam; further, Putnam and Putnam place their cortical area of binocular vision anterior to their monocular area, and the degeneration technique failed to reveal the presence of a second area of representation, either in the cortex or in the geniculate nucleus.

Using the increased precision of topographical localization available by this method, Thompson, Woolsey and Talbot drew attention to the spacing of their degree contours when projected on the cortex. In their map - derived from a composite of fine experiments - the even spacing of the contours showed no enhanced resolution in the vicinity of true lateral vision, whereas an increased spacing

between the contours, in an area corresponding to the nasal edge of the retina, indicated an area of enhanced resolution developed for rearward vision. Their map of the cortical projection attributes to the rabbit an extensive field of monocular vision in the horizontal plane, the vertical extent however being extremely limited, confined to about 15° above the horizontal plane and 20° below it. The projection of such a field on to the cortex would imply a gross distortion of the "circles" of latitude of the field and retina, these undergoing transformation into ellipses on the cortex; this would imply, too, a significant difference between the magnification factors along the vertical and horizontal meridians, these features remaining unrecognized by Thompson, Woolsey and Talbot due to their use of linear field coordinates. Their failure to observe an increased area of representation along the axis of the eye is, however, more significant for Chievitz 1891 and Slonaker 1897 had described an area centralis retinae in the form of a narrow band lying below, and parallel to, the myelinated band of optic nerve fibers.

B. Cat.

Talbot 1940, Talbot and Marshall 1941, using a flash subtending 20' of arc at the eye, mapped the projection of the visual field on the cat's cortex, recording the evoked potentials with a moist wick or needle electrode and found each hemi-cortex receiving projections from the contralateral half fields of both eyes, the line of division splitting the fixation point. The vertical meridian was represented up to 40° below fixation point and 20° above it, the horizontal to more than 50° from it. The vertical meridian on the cortex follows a line diagonally along the lateral gyrus in the lower field, and to the bottom of the posterolateral sulcus in the upper field, the entire contralateral visual half fields being represented medial to this line. Talbot 1942 described a second functional localization lateral to this line, oppositely disposed and confined anteriorly to the lateral gyrus and posteriorly to the supra sylvian where the exposed cortical surface affords access to corresponding points in a small area of the upper field; for other field areas, one or both of the corresponding cortical loci are buried.

The representation of the field in the second area was found to be equally accurate, optic nerve

stimulation or retinal flashes producing virtually identical responses with respect to the latency of the primary wave and the latency and amplitude of the "off" wave. The lateral area was not depressed by narcosis of the medial area and fired independently of local stimulation by convulsants, of its ^{medial} ^{area} ~~topographical~~ ~~opposite~~, Talbot believing this evidence to be suggestive of a separate sub-cortical projection.

Doty 1958, using diffuse flashes of light shone directly into the eye, recorded the evoked cortical surface responses from several areas lying far beyond those included within the histological limits of the striate cortex, confirming O'Leary 1941, who, studying the histology of the striate cortex, drew attention to the discrepancy between the boundaries of the optically excitable cortex and the cytoarchitectonic limits of the striate cortex. This fact, together with his observation that the potentials evoked by flashes or electrical stimulation of the optic nerve were much larger in amplitude in the cortex, adjacent and lateral to the area striata, than they were in the striate area itself, and that extirpation of this high amplitude region did not produce retrograde degeneration of the lateral geniculate

nucleus, led Doty 1958 to argue that "the topographical arrangement of retino-cortical projection is in itself of minor or no importance in the visual analysis of geometric patterns." Doty 1961, however, admits of the inadequacy of his experimental technique; the use of light sources, fixed 10° apart giving diffuse flashes, in view of Hubel and Wiesel's 1959 demonstration of the effects of peripheral illumination exerting lateral inhibition on small central receptive fields; the error of projecting large flashes directly at the animal's eye, in view of the extent of intraocular scattering of light by the highly reflective tapetum of the cat's eye; and with his failure to choose only the shortest latency responses as a criterion of localization.

Doty 1953 quotes the evidence obtained from behavioural experiments, that cortex other than striate is necessary for visual pattern discrimination in cats with extensive damage to the geniculostriate system, and that normal visual abilities develop in the complete absence of the striate system in cats from which this area is removed at birth - and concludes "that there may conceivably exist two processes, one which rapidly affects the cortex in a topographically arranged manner, and a second which is a slower, possibly intraretinal

process, which elaborates the stimulus over a much wider cortical area". and Allen 1943, who suggest that

Vastola 1961, stimulating the optic nerve electrically, elicited from the medial lip of the middle part of the suprasylvian gyrus of the contralateral cortex a short latency response, varying in amplitude by the same amount and in the same direction as does the simultaneous response in the striate cortex. The suprasylvian response was not changed by isolating the ipsilateral lateral geniculate nucleus from the pretectal and medial thalamic nuclei, by isolating the ipsilateral postero-lateral, splenial, or suprasplenial gyri, or by destroying the contralateral geniculate nucleus or tract; the response being abolished, however, by anodal polarization of the ipsilateral geniculate nucleus. These observations suggest that the suprasylvian area represents a direct pathway activated by fast fibers from the ipsilateral geniculate and that the striate cortex, which receives the primary radiation fibers, is but a part of a considerably larger cortical field innervated by secondary radiation fibers, and that the extrastriatal portion may well mediate those modalities of vision which persist after total extirpation of the striate cortex.

These observations are in agreement with those of Marshall, Talbot and Ades 1943, who suggest that the suprasylvian gyrus responses are of two types - responses evoked via association paths from the striate cortex, and those that show characteristics of a primary projection pathway from the geniculate. The second type of response persists after ablation of both cortices and section of the collicular bound pathways, and fail after retrograde degeneration of the geniculate nucleus consequent to extirpation of the striate cortex, yet no clear degeneration of the geniculate is seen after circumscribed lesions of the suprasylvian gyrus.

Clare and Bishop 1954 demonstrated a fairly limited "point to point" relationship between the suprasylvian region and the primary visual cortex, but believed the suprasylvian to be a secondary projection from the striate cortex, whereas Buser and Borenstein 1956, 1957 believed the suprasylvian response to be mediated by a projection from the posterior or postero-lateral thalamic nuclei, medial to the lateral geniculate nucleus and innervated by fibers from it.

C. Monkey.

Talbot and Marshall 1941 mapped the central

part of the visual field on the postero-lateral surface of the exposed cortex, expressing the index of cortical representation as the increment of the angle measured radially from the center of gaze represented on each millimeter of cortex.

Daniel and Whitteridge 1961, using steel needle electrodes and a source of light subtending 10' arc at the eye, confirmed the observations of Talbot and Marshall and extended the mapping to the cortex buried in the horizontal and vertical calcarine fissures. Using as their index of cortical representation a factor M (i.e. millimeters of cortex concerned with 1° of the visual field), they determined quantitatively the extent of cortex devoted to the separate regions of the visual field and determined the relationship between the magnification factor at a point, and its eccentricity, measured radially away from the center of gaze. Since, also, they found no significant difference between magnification factors measured along different radii, the distorted lengths of each semi-circle of latitude when projected on the cortex could be calculated, so too for the distorted length of the horizontal meridian as projected on the cortex. These provided the dimensions of a model, the surface of which could then be "folded" to give a close approximation to the size and folding of the visual cortex.

4. Sub-Cortical Visual Activity in the Cat.

(i) The Eye.

The cornea of the cat forms a prominent curve, subtending nearly 170° of arc, and with the angular extent of the retina and a wide pupillary aperture combine together to give the cat a uniocular field of about 200° in the horizontal plane. The frontal position of the eyes in the head, with a relatively narrow angle between its optic axis and fixation axis (the alpha angle being 13°), gives the cat a field of binocular vision of 120° , and hence an exclusively uniocular field of 80° for each eye and an 80° blind field posteriorly.

The wide extent of a uniocular field, with a consequent diminution of the binocular field, seems biologically determined by the need of a panoramic view for the hunted animal, whereas the extent of binocularity, on the other hand, seems determined by the greater value of fine judgment rendered possible by binocular vision; for pursuit and attack by the predatory Carnivores, or in Primates, for accurate correlation with the use of its forelimbs, Duke-Elder 1958. In addition to the biological value of binocular vision as an asset to predacity and fine manipulation, an increase in sensitivity to light may be a third factor in determining its acquirement - Weale 1955, the

binocular sensitivity to light being greater than the unocular by 10% in Man, Pirenne 1943. This may account for the parallelism of the visual axes in some predominantly nocturnal types, cat, owl and certain deep sea fish with tubular eyes, these animals compensating for the loss of panoramic fields by a significant increase of light sensitivity.

Ingvar 1959 quotes Willmer 1955 and describes the cat retina as resembling that of the human peripheral retina. Schultze 1866 observed the rod-cone ratio in the cat to be 2-3 times that of the human periphery. Marriot, Morris and Pirenne 1959, using the data of Schultze 1866 and Osterberg 1935, estimated the rod content of the cat's retina to be 23.8 million/square cm., their own estimate being 46 million/sq. cm.; they, however, give no indication of the locus in the retina wherein these counts were made. Rochon-du Vigneaud 1943 quotes Thieulin's 1927 estimate of the rod-cone ratio in the cat's peripheral retina to be 25:1.

The structural perfections of the axial region of the retina are minimal, being expressed as a more or less pronounced refinement of the receptor cells - the elements here being narrow and short, the rod-cone differences are minimal; a moderate accumulation of ganglion cells and an arching course of

blood vessels away from this area. Chievitz 1891 describes an area centralis retinae in the cat, as does Ganser 1882 and Slonaker 1897. Krause 1891 describes an area centralis as well as a true fovea. Duke Elder quotes Zurn 1902 who describes a small temporal round area of highly differentiated visual elements closely packed together with an accumulation of ganglion cells packed in several layers. Polyak 1943 describes a shallow rudimentary or perhaps orimantal fovea, associated with the typical arching course of nerve fibers. Chievitz 1891 and Slonaker 1897, however, could find no definite evidence of a true foveal region. Rochon du Vigneaud 1943, after Thieulin 1927, describes a small area about 1 mm.sq., 3 mm. temporal to the optic disc and in line with its upper border containing only cones, the retina immediately adjacent to this area having a rod-cone ratio of 1:20. Ingvar 1959, quoting Abelsdorff 1905 and Kolmer 1936, asserts the presence of an area centralis with a higher percentage of cones than in the adjacent and peripheral retina. Uyama 1934 studied the details of distribution of the large horizontal cells of the cat's retina; the highest concentrations of these cells were found in the region immediately temporal to the optic disc, i.e. in the region of the area centralis; the cell content in the central regions

of the retina were significantly higher than in the periphery, but there was no significant difference in the distribution of these cells in tapetal and extra-tapetal retinae.

Ganser 1882 describes the arcuate course of the optic nerve fibers skirting a conical mound of accumulated ganglion cells formed at the central area, the distance from the edge of the optic disc to the peak of the mound being given as 2.4 mm. and 2.8 mm. in two cats. Bishop 1953, Bishop, Jeremy and Lance 1953 report total ganglion cell counts in the cat retina to be 120,000, a figure closely approximating their fiber count for the optic nerve. Bishop, Kozak and Vakkur 1962 describe the appearance of the area centralis in methylene blue stained preparations of the intact retina. The dense collection of ganglion cells demarcates the area centralis as a small area, less than 1 mm. in diameter with a less dense temporo-superior extension. Two classes of ganglion cells were made out, large and small; except for the area centralis, both types of cell seem to be fairly uniformly distributed in the fundus, the small cells being much more numerous than the large. Towards the periphery of the retina, however, they observed the density of ganglion cells to be markedly reduced.

Bishop, Kozak and Vakkur 1962 establish the relative positions of the area centralis and optic disc in the cat fundus. The area centralis is identified ophthalmoscopically by observing the characteristic arrangement of blood vessels in comparison with the known patterns of vessels, disc, and ganglion cell concentrations in stained intact retinae. The positions of the area centralis and optic disc are plotted on a tangent screen and found to subtend an angle of 16.1° between them. Taking 4.4° of visual angle as equivalent to 1 mm. on the retina, the angular distance of 16.1° gives a retinal distance of 3.6 mm. which is in close agreement with the distance of 3.4 mm. obtained by direct measurement in stained intact retinal preparations. The mean location of the blind spot with respect to the fixation point is given in spherical polar co-ordinates with axis through the reference point as a deviation angle of 16.0° and elevation angle of 24.4° , without any significant assymetry between the two eyes.

Viewed ophthalmoscopically the tapetum is seen as an extensive triangular area occupying most of the posterior polar region of the eye. The base of the triangle is almost horizontal and lies a short way beyond and below the level of the disc, the apex of the triangle lying in the upper pole

of the eye. The tapetum gives the retina associated with it an irridescent greenish yellow colour, but towards the tapetal edge the colour changes to a deep greenish violet, then to a deep brown - the colour of the peripheral retina. Walls 1942 attributes these colours to interference phenomena, as does Weale 1953, though Gunter, Harding and Stiles 1951 attribute it to the presence of pigment in the tapetal cells. The tapetum lies between the sub-retinal chorio-capillaris internally and the choroid externally and consists of closely set layers of thin, flat, rectangular cells of endothelial origin, arranged in precise and orderly tiers. In the central polar region the tapetum is of greatest thickness, the cells being packed 30 deep; from this region the layers thin out towards the periphery of the tapetum, Campbell 1961.

The retinal pigment is almost totally absent in the tapetal region. From an optical point of view, the tapetum has been considered by Campbell 1961 to be a concave mirror situated behind the upper quadrants of the retina, reflecting back on to it the light that has passed through the dioptric media. Polyak 1943, Du Vigneaud 1943 and Duke Elder 1958, view the tapetum as a device serving to increase the retinal sensitivity to light in this predominantly nocturnal animal. Gunter

Harding and Stiles 1951, studying the reflection factor of the excised tapetum, found the maximum reflection of incident light amounted to 25% in the blue part of the spectrum and concluded that the overall percentage of reflected light was too small to play an appreciable role in modifying retinal sensitivity. In contradistinction, however, Granit 1943 believed that the tapetum in situ was an efficient reflector, and Weale 1953 finds the tapetum in situ to have a marked effect on threshold, though it did not alter the spectral sensitivity curves under scotopic or photopic conditions. Dodt and Walther 1958, investigating the photopic dominator responses in the E.R.G. found that 0.45 to 0.75 log units more light was required to evoke E.R.G. responses of the same size from extra-tapetal, in comparison with tapetal retina; they, too, confirm the view that the tapetum has no effect on spectral sensitivity. The value of these observations is, however, limited by the fact that comparative values of tapetal and extra-tapetal responses should be made at positions in the retina corresponding to exactly comparable points in the visual field.

Gunter 1951, using behavioural discrimination methods, expressed the absolute threshold of vision in the cat as 9.92×10^{-8} milliLamberts; under identical conditions the human threshold was

5.47×10^{-7} mL, a figure in close agreement with that given by Bridgeman and Smith 1942, 5.8×10^{-7} mL. Gunter attributes the greater light sensitivity of the cat to several features in the cat's visual system; the higher rod-cone ratio, the presence of a tapetum, the relatively large aperture of the fully dilated pupil, and the finding of Glees 1941 of a considerable degree of overlap in the synaptic terminals of the optic tract fibers on the neurones of the lateral geniculate nucleus.

Marriot, Morris and Pirenne 1959, recording the activity of single units in the cat's lateral geniculate, determined the absolute threshold of vision and report a value of 7.4×10^{-7} ergs/sec./cm.² threshold, being expressed in energy units at the retina. Using the data of Gunter 1951, they express the threshold obtained from behavioural experiments as 2.4×10^{-7} ergs/sec./cm.², and attribute the threefold increase of threshold in their experimental animals to the effects of anaesthesia, surgical procedure, and their likely failure to have sampled the most sensitive units. Marriot et al 1959 estimate the human threshold to be 9.09×10^{-8} ergs/sec./cm.², i.e. almost two and a half times as sensitive as the intact unanaesthetized cat.

Barlow, FitzHugh and Kuffler 1957, recording

the activity of retinal ganglion cells in the cat, determine the absolute threshold of vision to be 520 - 3300 quanta/sec./degree of solid visual angle. Using the data of Gunter 1951, they find for the intact cat a value of 96 quanta, and for the human, 23 quanta/sec./degree of solid visual angle.

Rochon du Vigneaud 1943, Duke Elder 1958, recognizing the features of the cat's visual system that give it an enhanced degree of retinal sensitivity, remain dubious of the popular belief of its excellent nocturnal acuity. Du Vigneaud doubts whether a cat is able to see a stationary man at 12 meters "in the dark" and mentions that when deprived of whiskers the cat walks in the dark with much greater hesitancy and caution. Duke Elder 1958, expressing acuity in terms of the minimum angle of resolution, attributes a relative value of 5.5 minutes of arc to the cat, and 0.44 - 0.8 minutes of arc to Man, under photopic conditions.

Retinal Interaction.

The pioneer experiments of Adrian and Matthews 1927 with the eel retina demonstrated the interaction of retinal units and introduced the modern phase of the subject. Hartline 1938, studying vertebrate optic nerve fibers, showed that they

were of several functional types, with respect to their responses to illumination of the retina. He found fibers which produced a sustained discharge during illumination, others which responded only at "on" and at "off", and a third group which gave only "off" discharges. Each fiber was found to have a retinal receptive field whose size was variable and dependent on the intensity and area of illumination and state of light adaptation. Granit 1933 proposed the occurrence in the retina of an inhibitory process and Kuffler 1953 observed it in the cat retina. It was shown that the discharge patterns of a ganglion cell varied with a number of factors such as background illumination, position, pattern, intensity and area of stimulation; from the same cell "on" "off" and "on-off" responses could be recorded according to the position of the stimulus in the receptive field. The fields were found to be arranged in a special way, the central area of lower threshold being either "on" or "off" and the peripheral surround conversely "off" or "on", with an intermediate "on-off" zone between them. Kuffler observed mutual interaction between central and peripheral zones; the center could inhibit the periphery, and the periphery could inhibit the center, or each could reduce, under appropriate conditions, the others' discharge, depending on the

relative intensities of the two stimulating spots. Wiesel and Brown 1958 showed that different receptive fields of the cat's retina differ in certain quantitative respects, especially in the degree of suppression of the center by the surround. Regional differences in receptive fields were also noted; the ganglion cells of the area centralis tended to have smaller fields, subtending about 0.5° at the eye in comparison with fields of ganglion cells of the peripheral retina which subtended $8-10^{\circ}$ at the eye, a feature probably related to the higher visual acuity of the central retina.

Barlow, FitzHugh and Kuffler 1957 showed that the organization of the receptive fields underwent a change in passing from the light to the dark adapted state. Contrary to previous ideas, which postulated an increase in summation area, the main effect of dark adaptation was found to be the disappearance of the peripheral antagonistic field. Thus an "on" center field with an "off" periphery became a simple "on" center - the actual size of this field decreasing in size during the process of dark adaptation. Brown and Wiesel 1958 describe another type of retinal response, called "pure inhibition", since there were no "off" discharges associated with it. A stimulus in the center of such a receptive field completely inhibits

the maintained resting discharge, but with adaptation some activity returns despite the continued illumination; when the light was then turned off, inhibition of the activity again took place, without any "off" discharge.

Under scotopic conditions, the retinal spectral sensitivity (i.e. reciprocals of the intensity producing equal responses, as determined by size of wave in the E.R.G. spike frequency etc.) of the cat shows a fairly good correspondence with the absorption curve of rhodopsin which is probably identical with the visual purple of the cat.

Receptor mechanisms underlying this broad curve were called the scotopic dominator, Granit 1943. Differentiating rods and cones with the aid of their specific spectral sensitivity curves, Granit 1943 recorded from the ganglion cell and provided proof of Polyak's generalization that in "mixed retinae" rods and cones could discharge into "the optic nerve through the same ganglion cell."

In the light adapted retina about 36% of retinal elements were found by Granit 1945 to demonstrate another broad sensitivity curve, with a maximum at 550-560 milli-microns. This curve represents the photopic dominator of the cat and was considered responsible for the Purkinje shift of spectral sensitivity. Under conditions of weak

white light or selective monochromatic adaptation, further narrow banded humps on the broad photopic dominator curves were demonstrated; these modulator maxima were found in three preferential regions 440-460 milli-microns, 520-540 milli-microns, and 580-600 milli-microns.

Meyer, Miles and Ratoosh 1954, however, using behavioural tests, showed that when odour position and brightness clues were eliminated cats could not discriminate between the spectral colours. Walls 1953, commenting on the presence of colour sensitive units in the cat retina, suggests that "it may have a very important physiological significance, though not in relation to the animal's colour vision" - Walls quotes the reports of Donner and Willmer 1950 who found that "on-off" fibers which show modulator characteristics show maximal spiking activity at one time or another, in one of three particular places, in the time course of its off discharge, depending on the wavelength of the stimulating light. These maxima keep their relative time positions when the intensity of the stimulating light is changed, and the wavelengths producing the sharpest positioning of these impulse bursts were in the same regions in which Granit found the peaks of his modulator curves. Commenting on these findings, Walls suggests that "the cat's modulator

mechanisms may afford a means of causing a dispersal of events along a time scale in the transmission of visual information. If spectrally different stimuli are enabled to generate impulses in imitation of the modulations of the frequency-intensity functions in the paths, then the whole pattern of the stimulus is more elaborately 'coded' than it could otherwise be. In such a system chromaticity differences at equal luminance, as well as luminance differences at identical chromaticities, are enabled to generate brightness differences in the pattern perceived".

(ii) The distribution of the optic nerve and tract.

Bruesch and Arey 1942 believed the optic nerve of the cat to contain about 118,000 fibers, most of them myelinated. Bishop, Jeremy and Lance 1953 give counts of 120,000 and claim all to be myelinated, but more recent electron microscope studies of the anuran optic nerve, Maturana 1959, suggest that earlier estimates of fibers, based on light microscopy, may be largely in error. The study of conduction velocities, and pre and post synaptic tract responses, have led to very divergent views with respect to the segregation of fiber groups in the optic nerve and tract.

Bishop, Jeremy and Lance 1953 describe two groups with a well marked segregation of the fibers according to size - only small fibers being present in the upper part of the nerve and tract, the larger fibers being concentrated into the lower part. The large fibers being 3-8.5 microns diameter with conduction velocities of 30-40 meters per sec., the smaller fibers 1-2 microns and conducting at 15-20 m./sec. Chang and Kaada 1950, and Lennox 1958 claim segregation into three groups, while Bishop and Clare 1955 claim four groups; the largest fibers being 8-12 microns diameter, conducting at 40-50 m./sec. and destined for the dorsal laminae of the lateral geniculate, the second group with fiber diameter of 4-8 microns, conducting at 15-25 meters/sec. ending in the ventral lamina B of the pars-dorsalis, while the two groups of thinner fibers were less than 4 microns, conducted at less than 12 m./sec. and terminated in the tectum, pretectal and collicular regions. Hayhow 1958 could find no evidence of such a segregation; Le Gros Clark 1962 denies that such a segregation according to fiber size, or function, or locus of destination exists, claiming that unshuffling of the fibers from a common mass takes place only when the geniculate nucleus is reached. Maturana, Lettvin, McCulloch and Pitts 1960 agree with this view,

claiming that in the optic nerve of the frog the fibers are randomly distributed, congregating again only at their terminals according to their points of origin and function, while Hoyt and Luis 1962 observed macular fibers from the retina of the macaque mixing freely with those of the peripheral retina in all parts of the anterior visual system. About 30% of the optic nerve fibers remain uncrossed in the chiasma, the intermediate bridge-like portion of the chiasma being formed by the crossing fibers originating from the two slightly larger nasal halves of the two retinae; the decussating bundles turn towards each other and interweave in a complicated fashion as they cross to the opposite tracts, Polyak 1959.

The main bundle of the optic tract reaches the level of the lateral geniculate nucleus, and then bends sharply medial to pass under the nucleus proper at the lower apex of the ventral portion of the geniculate. Cajal 1911, Thuma 1928, Barris, Ingram and Ranson 1935, O'Leary 1940, Bishop and O'Leary 1940, Bishop and Clare 1955 agree that the division of the tract reaching the pars-dorsalis contains most of the largest fibers of the tract. Bishop and O'Leary, Bishop and Clare, also claim that together with these large fibers are some smaller fibers destined for the layer B of the pars-

dorsalis. Cajal 1911 observed thin collateral branches of these thick optic fibers reaching the pars-dorsalis, but was unaware of their destination; Barris, Ingram and Ranson, O'Leary and Glees 1941, were of opinion that these thin collaterals reached the superior colliculus and pre-tectal regions, whereas Bishop and Clare believed that the collicular and tectal fibers constituted a structural and functional entity maintaining their identity from the retina onwards. Cajal believed that the colliculus was innervated by a special variety of retinal afferents and that thin collaterals of these fibers supplied the pars-ventralis, the pars-ventralis itself receiving no contribution from the thick afferents reaching the pars-dorsalis. Minkowski 1920 and Thuma 1928 found a few thin crossed fibers reaching the pars-ventralis, Barris Ingram and Ranson could trace no afferent supply to it, whereas O'Leary and Hayhow 1958 found collaterals of the thin tract afferents reaching the pars-ventralis from the ipsi and contra-lateral retinae.

Polyak 1959, tracing the afferent supply of the pregeniculate nucleus, found them to arise in the central areas of the retinae of ipsi and contra-lateral eyes, but was uncertain whether these fine myelinated fibers were the axons of a special

variety of retinal ganglion cells, or whether they were collaterals of 'central' axons passing to the pars-dorsalis.

After the passage of the thicker fibers to the pars-dorsalis, the remaining tract consists mainly of fine fibers with a few medium sized ones; these form a sheet which invests the pars-ventralis, especially on its ventral and posterior surfaces, and then envelopes the ventral and posterior surfaces of the pars-dorsalis; from here the fine fibers continue caudally, forming a narrow compact intergeniculate lamina separating the lateral geniculate and pulvinar on the lateral aspect from the medial geniculate nucleus on the medial side. Further, postero-medially this lamina splits into two and in cross section beyond the lateral geniculate nucleus the tract appears V shaped, with a fin extending medially towards the pre-tectal region, about as far caudally as the level of the habenular nuclei; the fibers then turn ventrally into the pre-tectum; the cells lying along and below this fiber tract appear to be the synapse stations for these afferents, Polyak 1959, Ranson and Magoun 1933. The other fin of the intergeniculate fiber lamina lies ventral to the medial border of the pars dorsalis where it becomes continuous with the posterior portion of the pulvinar;

the fiber tract then runs posteriorly and medially to reach the superior colliculus by way of the brachium of the superior colliculus. Studying the responses to electrical stimulation of the optic nerve and tracts, Bishop and O'Leary 1940 indicated that between the geniculate and colliculus there lie various structures - the pulvinar, the nucleus lentiformis and the nucleus mesencephali - which receive optic tract afferents. They also traced such fibers to the marginal territory along the tract bordering the medial geniculate nucleus and the territory just medial and anterior to the pars-dorsalis of the lateral geniculate. They report that in these regions the post-synaptic responses were very well localized, the movement of the critical electrode 0.5 mm. in the vertical plane determining their presence or absence.

(iii) Histological studies of the Lateral Geniculate Nucleus.

The morphological characteristics of the cat's lateral geniculate nucleus have received a great deal of attention. The investigations have employed four main neurohistological techniques:-

1. Studies on normal material; by Tello 1904, Cajal 1911, Taboada 1927 and O'Leary 1940

using golgi stains, and by Thuma 1928 using Huber's Toluidine blue.

2. Demonstration by the Nissl method of trans-neuronal degeneration after section of one optic nerve. Minkowski 1920, Barris, Ingram, Ranson 1935 and Cohn 1956.
3. Marchi studies to show course and distribution of degenerating optic axons resulting from experimental lesions of the retina or section of one optic nerve. Minkowski 1913, Brouwer and Zeeman 1925, Overbosch 1927, Barris 1935, Cook and Barr 1950.
4. Special silver stains to reveal terminal degeneration of optic afferents on the geniculate cells. Glees 1941, Fillenz 1961.

Hayhow 1958, 1959, in a comprehensive study, enucleated one eye and used the Nauta-Gygax, Cajal, Bielschowsky, Nissl, and Glees stains to study the geniculate nucleus in relation to the distribution of crossed and uncrossed optic fibers, the differences in synaptic terminations in the different regions of the nucleus and in optic fibers of differing size.

The lateral geniculate nucleus consists of three discrete elements:-

1. The pars dorsalis.

2. The pars ventralis.
3. The nucleii perigeniculatus, anterior and posterior.

The Pars Dorsalis.

In para-sagittal section, the pars-dorsalis is a convoluted cellular mass of S shape, the posterior and dorsal limb of the S consisting of an almost vertical plate of cells, with its long axis lying in the transverse plane. The bulk of the pars-dorsalis consists of the basal limb of the S, a relatively thick plate of cells, almost semi-spheroidal in shape, lying in the horizontal plane at right angles to, and becoming continuous with, the posterior and dorsal vertical plate of cells. The pars-dorsalis has been thought to consist of three cellular laminae, separated one from another by two sparsely cellular, inter-laminar fiber plexuses by Tello, Thuma, O'Leary, Hayhow and Silva, whereas Barris 1935 has discerned in it ⁴four layers in agreement with that described in the dog by Rioch 1929. The various descriptions, however, are essentially equivalent and differ only in terms of discreteness accorded to the layer of large cells present between the two ventral laminae, A₁ and B. These two laminae have each a characteristic cellular structure and are separated from each other, not by a prominent medullary lamina,

comparable with that of the more dorsally placed AA₁ interlaminar fiber plexus, but rather by a cellular transitional zone characterized by the presence of scattered, large, deeply staining cells. These large cells, together with the similar large cells present in the AA₁ interlaminar plexus, were considered by Thuma to be sufficiently unique to warrant the application of a special name, the 'nucleus interlaminaris centralis'. In Nissl stained sections of the dog's geniculate, Rioch described a discrete lamina magnocellularis lying immediately ventral to the A₁ lamina. O'Leary 1940, using golgi stains in the pars-dorsalis of the cat, substantiated Rioch's observations, commenting however that a similar distinction between magnocellular and parvocellular laminae is not as readily made in the cat, the larger cells being fewer and more diffusely scattered. Barris 1935, using Rioch's terminology, described the lamina magnocellularis in the cat as a thin and somewhat irregular layer of large cells present in the thickened anterior segment of the pars-dorsalis, being completely absent in the posterior segment where the laminae are aligned one behind the other.

In addition to the nucleus interlaminaris centralis, Thuma described a diffuse cluster of cells situated between the pars-dorsalis laterally and

the pulvinar medially; dorsally and ventrally this poorly defined plate of cells was limited by the rami of the optic tract, this group of small cells being named the nucleus interlaminaris medialis.

A similar intermingling of cells in the postero-medial region of the pars-dorsalis with those of the pulvinar has been described in the dog by Rioch.

Hayhow 1958 has shown that the region of the nucleus interlaminaris medialis is constituted by three poorly defined vertically orientated bars of cells continuous with those of the pars-dorsalis, and, on account of the general similarity in the distribution of the ipsilateral and contralateral optic fibers within the pars dorsalis and this medial "interlaminar" nucleus, viewed this latter as a relatively independant, accessory pars-dorsalis.

There is general agreement - Minkowski 1920, Barris 1935, Overbosch 1927, O'Leary 1940, Cohn 1956, Silva 1956, Hayhow 1958 - that in the cat the optic fibers of crossed and uncrossed retinal origin terminate in different and alternate dorsalis, the contralateral fibers ending in the two outer layers A and B, the ipsilateral fibers in the central layer A_1 . The completeness of this segregation, however, is in dispute, O'Leary being of opinion that the cells of a lamina were exclusively innervated by fibers of one retina or the other,

and that the dendrites of the short axon cells of a lamina did not invade the adjacent lamina. The Marchi method, however, does not stain the fine terminal arborizations of the tract afferents and in a nucleus where there is normally a wide range of cell size this technique can only reveal gross overall changes; Hayhow, using Nauta-gygax and Glees stains, claims the existence of binocular overlap in the region of the nucleus interlaminaris centralis and the nucleus interlaminaris medialis. The large cells of central interlaminar nucleus separate laminae of characteristic cellular structure which receive preterminal fibers derived entirely from the ipsilateral or contralateral retinae, but the cells of the interlaminar nucleus itself are supplied by preterminal fibers from each of the two laminae that they separate. Hayhow reports that the most extensive intermingling occurs in the medial interlaminar nucleus, while, with respect to the dorsal and ventral components of the nucleus interlaminaris centralis, the extent of overlap is probably greater in the large celled ventral component than in the dorsal.

Although an overlap in the terminal distribution has been demonstrated, different interpretations may be placed on this finding. First, that there may exist a true binocular afferent

supply to each principal cell concerned: or that one principal interlaminar cell may be innervated exclusively by crossed fibers, while an adjacent interlaminar cell is supplied by afferents derived entirely from uncrossed fibers, thus effecting an interdigitating relationship between the laminae and thereby extending the feature of intralaminar segregation into the interlaminar regions. Fillenz 1961, reinvestigating this problem, used the Glees silver stain and believed the appearance to be suggestive of binocular convergence into a single geniculate cell.

The two dorsal laminae A and A₁ are of identical histological structure and are separated throughout their extent by the AA₁ interlaminar fiber plexus. Anteriorly, where the laminae are horizontally disposed, they are 20-25 cells thick, but posteriorly, where the laminae are vertical, each is greatly reduced in thickness, being here less than 10 cells thick. The laminae are characterized by a fairly uniform distribution of small (10-20 microns), medium (20-25 microns) and large (30-40 microns) cells, in numbers inversely proportional to their sizes. Hayhow 1958, 1959, confirms the views of Tello 1904, Cajal 1911, Taboada 1927, O'Leary 1940, Bishop 1953, who have described the cells in the pars-dorsalis as belonging to two

main types, principal and short axon cells respectively. The principal cells are those whose axons enter the optic radiation, while the short axon cells have processes confined to their laminae of origin. The cells tend to be aggregated into small clusters or glomeruli containing some six to eight cells; their dendrites arising from several shafts, branch extensively at their origin to give rise to an exceedingly dense protoplasmic plexus. The dendrites of cells whose bodies are situated away from the surface of a layer arborize in all directions, the cells situated near the surface of a layer having most of their dendrites directed towards the center of the layer. O'Leary 1940, found the short axon cells scattered throughout the three laminae, but in all cases the distribution of the axons and dendrites was limited to the layer in which the cell body was situated.

O'Leary observes that the random distribution and mutual interlocking of the axons and dendrites of these cells would probably prevent any effective electrical fields being set up when they became active, and that self-reactivation was not an important phenomenon in the lateral geniculate body of the cat for fast conduction through the nucleus with no sequelae of sustained activity has been observed, suggesting that though the short



axon cells could not play the role of inter-neurons in the pars-dorsalis, they may instead act as synchronizers for groups of principal cells.

The manner of termination of the optic tract within each of the two dorsal laminae has been studied by several - Tello 1904, Taboada 1927, Bishop 1953, Hayhow 1958. The large optic afferents form initially a tangentially orientated axonal plexus which envelopes the large cells of the nucleus interlaminaris centralis; from here the tract fiber continues to its layer of termination and, reaching it, bifurcates repeatedly, but the terminal branches retain a predominantly parallel orientation directed towards the surface of the lamina, producing a "cypress tree" type of arborization. The arborizations of several optic fibers together form a dense fibrillary glomerulus in the meshes of which are embedded the cluster of six to eight principal cells - the cellular glomerulus of Taboada. Glees 1941, studying the terminal degeneration of optic afferents in these two laminae, demonstrated that in the mature animal at least the optic fibers end in the nucleus in special end-formations in the shape of fine terminal rings, and that each principal cell established contact with at least forty of these optic terminals, axodendritic contacts being more numerous than the

axo-somatic, and that the terminal brush of each afferent fiber lies in relation to about ten principal cells. Commenting on this extensive overlap, Glees writes "the profusion of terminal boutons in the geniculate body of the cat, together with the overlap which appears to exist, would provide an anatomical basis for a high degree of sensitivity in low intensities of illumination". Granit 1962 quotes Bishop 1953 and claims the total number of cells in the cat's pars-dorsalis to correspond roughly with the total number of fibers in the optic nerve, whereas Brindley 1960 attributes to Bishop 1953 a value of 450,000 cells in the pars-dorsalis; Bishop 1953, reporting only that his total ganglion cell count in the retina of 125,000 corresponded closely with his optic tract fiber count of 127,000!

These ratios lead Brindley to suggest that the pars-dorsalis does not "compress visual information into a smaller number of channels, on the contrary there is little doubt that the number of cells in the geniculate body - and therefore presumably in the geniculo-calcarine tract - is greater than the number of optic tract fibers entering the geniculate body".

Yet, however, the fact that some optic tract fibers may not reach the geniculate body, the

presence of short axon cells in the pars-dorsalis, and the possibility that some cells of the nucleus are activated partly or exclusively by non optic afferents - (Hubel and Wiesel 1961) - makes these ratios of tract fiber - radiation fiber divergence uncertain. Further, Glees makes no mention of the locus in the geniculate wherein his observations were made, nor does he assert that it is a relation which holds for all regions, this feature leading to greater uncertainty whether the same ratios of "divergence" hold equally well for all parts of the pars-dorsalis.

The ventral lamina B is again of sigmoid shape, containing spindle shaped cells of medium size, 20-25 microns, separated ventrally by the layer of dispersing optic tract fibers and dorsally by the magnocellular layer and A_1B interlamina. It is of greatest thickness in the center of the anterior pole of the pars-dorsalis where the laminae are horizontal, being reduced in extent in the posterior vertical segment and almost absent in the extreme lateral and anterior aspects of the pars-dorsalis. Cajal, O'Leary and Hayhow have drawn attention to the histological features of this lamina which distinguish it from the A and A_1 laminae; its characteristic population of spindle cells, its afferent supply by predominantly small diameter fibers, and

the orientation of the terminal axonal arborizations in the plane of the lamina and not radially across it as they do in the A and A₁ laminae. These differences have prompted Hayhow 1958 to suggest the existence of a functional differentiation for lamina B, Bishop and Clare 1955 suggesting that the cells of this lamina project, not to the visual cortex but to the dorso-lateral portion of the intermediate or anterior region of the lateral nucleus of the thalamus.

The Pars Ventralis.

This is a small pyramidal mass of cells located between the medial and lateral rami of the optic tract, ventro-lateral to the pars-dorsalis and separated from it by a thin fiber layer; anteriorly it becomes continuous with the nucleus perigeniculatus anterior. It is composed predominantly of very small cells, 5-10 microns, scattered randomly in a dense network of nerve fibers.

Cajal, Minkowski, O'Leary and Hayhow find a few fine, crossed and uncrossed optic nerve fibers passing into the pars-ventralis, but in considerable areas of it they were either absent or very sparse, their appearances being taken to indicate that the pars-ventralis is predominantly supplied by afferent fiber systems other than optic.

The Perigeniculate Nuclei.

The nucleus perigeniculatus anterior is an attenuated irregular layer of small cells, forming a cap over the convex dorsal and anterior surfaces of the pars-dorsalis and separated from it by the fibers of the optic radiation, the nucleus perigeniculatus posterior forming a thin rim of small cells over the posterior curved surface of the pars-dorsalis. In the dog, Rioch describes a similar group of small disconnected, fusiform cells which nowhere could be regarded as a definite structure.

Polyak 1959 was of opinion that in the cat and monkey the perigeniculate nuclei received fine afferent fibers from ipsilateral and contralateral retinae, the fibers originating exclusively from foveal and parafoveal regions, but was uncertain whether these fine fibers constituted the axis cylinders of a special variety of retinal ganglion cells or whether they were thin collaterals of the thick foveal axons passing to the pars-dorsalis. Polyak believes that the axons of the perigeniculate cells constitute the perigeniculo-mesencephalic, or indirect opto-mesencephalic tract which pass posteriorly and medially into the subthalamic and pretectal areas.

The Electrical Activity of the Lateral Geniculate Nucleus.

Electrophysiological techniques have made possible the direct study of the responses of the lateral geniculate nucleus in response to electrical stimulation of the optic nerves and tracts, or to stimulation of the retina by light. These studies have had as their aims either collection of data to further understanding of the general problems of synaptic transmission in the central nervous system, or the finding of specific evidence relating to the flow of information in the central visual pathways. Crescitelli 1960 reviews the studies of synaptic transmission in the geniculate.

Cohn 1956, recording the responses of single units in the pars-dorsalis, confirmed the view obtained from histological studies that the middle lamina A₁ is connected functionally with the ipsilateral eye, the two outer laminae A and B having contralateral connections. Hubel and Wiesel 1961 confirmed this alternate arrangement of ipsilateral and contralateral connections and showed also that an electrode advancing normal to the anterior dorsal surface of the nucleus encounters successively geniculate neurones with receptive fields in almost identical positions. The units encountered in the three layers successively, being seldom separated

by more than a few degrees in homologous positions in the visual fields of the two eyes. Bishop, Kozak, Levick and Vakkur 1961 found that the contralateral homonymous half fields were represented on each nucleus, and that each region of the field was represented in the nucleus along a line obliquely penetrating the three laminae, these lines tending to lose their identity in the deeper parts of the pars-dorsalis because the receptive fields represented therein were large and ill-defined. They have also confirmed the gross details of topographical representation of the retina on the geniculate nucleus obtained by the earlier histological methods, finding in the left pars-dorsalis the nasal part of the right homonymous half fields projecting on to the medial aspect of the nucleus, and the temporal hemifield of the right eye on the lateral part of the nucleus, lower field on the antero-inferior aspect and upper field on the postero-superior, finding also that the central field occupies a very much larger region of the pars-dorsalis than does the peripheral field.

Erulkar and Fillenz 1956, 1958, 1960 report their observations of the activity of single units in the pars-dorsalis in response to diffuse flashes of light. Of 165 units studied 84% showed spontaneous activity in the dark, 57% behaved as "on-off"

types, 21% as "on", 6% as "off" and 5% showed suppression of their spike discharges during illumination. 11% of their units did not yield any response to illumination. Studying the effects of increased intensity of illumination on the latency of the single unit responses, they found decrement of latency in about 50% of their units and latency increases in 13%. These authors, however, make no mention of the loci in the pars-dorsalis from which their responses were obtained.

Hubel and Wiesel 1961, studying the single unit responses in cats anaesthetized with Sodium Penthobarbital and immobilized by succinyl-choline, stimulated the retina with a spot of light subtending 2° at the eye and with an annulus of light subtending 2° - 6° at the eye between its inner and outer borders. They observed that in their general arrangement the receptive fields of geniculate neurones resembled those of the retinal ganglion cells described by Kuffler 1953 and Wiesel 1960, the concentric fields having an excitatory center and inhibitory "off" periphery or the reverse; the two portions of the receptive field being mutually antagonistic, the inclusion of a part of the periphery causing a decrease in the size of the center response. All three layers of the pars-dorsalis contained "on" and "off" center units, A and A_1 being identical in their

firing patterns and average size of receptive field; in layer B, however, the receptive field centers were on the average several times larger than those in layers A and A₁, responses from B also being more "sluggish", with longer latencies and lower frequencies of firing. Bishop, Kozak, Levick and Vakkur 1961 report that the fields within or near the region corresponding to the area centralis retinae tended to have small field centers, generally 1°-2° across, with well-defined limits and were readily inhibited by their peripheral fields, in contrast to those cells having receptive fields in the periphery. Their views are in agreement with those of Hubel and Wiesel 1961 who describe small center "on" fields, situated in the central visual field, which are completely inhibited by the inclusion of even a part of their peripheral fields within the area of illumination. This phenomenon could readily account for the relative inefficiency of a diffuse flash as an effective stimulus. Enulkar and Fillenz 1960 found 11% of their units unresponsive, whereas Hubel and Wiesel find all the cells studied to be responsive to a small spot of light appropriately placed in the field. Studying the effects of the diameter of the stimulus spot on the latency and threshold of a center "on" response, they find that increase of spot diameter up to a critical

value reduces the latency of the response and the threshold value of the stimulus, further increase of spot diameter leading to an increase of response latency and threshold; indicating a summation of center "on" effects up to the critical value, further increase of spot diameter leading to the inclusion of the peripheral field, causing inhibition of the original center "on" effects. Erulkar and Fillenz's 1960 observations of latency changes in response to increasing intensity of illumination become explicable in this context.

Erulkar and Fillenz 1958, 1960 observed binocular interaction whilst recording from units in the interlaminar regions of the pars-dorsalis, some units responding to separate stimulation of either eye, while others showed modification of the response obtained from one eye by simultaneous stimulation of the other eye. This observation has been confirmed by Bishop, Kozak, Levick and Vakkur 1961, using stimuli of restricted size, and by Bishop and Davis 1953 who demonstrated binocular interaction by recording the responses of geniculate neurones to maximal contralateral optic nerve shocks before and after the application of a conditioning shock to the ipsilateral optic nerve. Hubel and Wiesel 1961, however, do not find any evidence of binocular interaction in any of the cells studied,

confirming the observations of Grusser and Saur 1960 and Grusser and Grusser-Cornehls 1961.

Hubel 1960 studied the responses of geniculate neurones, through implanted micro-electrodes, in the unanaesthetized cat. He observed that during sleep the units tended to fire in bursts, these short high frequency bursts occurring in clusters of 2-8 spikes at a frequency of 500/sec., the clusters recurring at rates of 0.5-5/sec.; since these units also gave responses to specific light stimuli, they were deemed unrelated to the effects of injury. The clustered pattern of firing could be abolished by light (they then behaved as "on" or "off" units) and by arousal of the animal from the sleeping state. The clustered activity was seen only during natural sleep and their abolition by arousal was not dependent on changes in the light reaching the retina, since the effect was reproducible during sleep and arousal in complete darkness. These clusters were not seen in the optic tract recordings, though grouped firing was a common feature in the visual cortex, Hubel 1959. The cortical bursts were, however, longer, less regular, and of lower frequency. Hubel comments, "it seems clear that the geniculate neurones can be influenced by means other than visual, though there is little to suggest which of the afferent

pathways to the geniculate mediates these arousal influences."

Bartley 1960 quotes Hernandez-Peon, Scherrer and Velasco 1956 who used electrodes implanted in the brain stem reticular formation, optic tract, lateral geniculate body and optic radiation, and were able to analyse the inhibitory effects of intercurrent brain stem stimulation on the relay of a flash evoked response from the retina to the geniculate and cortex; Dumont and Dell 1958 observed inhibition of the post-synaptic tract response in the geniculate neurones, produced by electrical stimulation of the optic chiasma during simultaneous stimulation of the brain stem reticular formation.

Niemer and Jiminez-Castellanos 1950 investigated striato-geniculate connections by Dusser de Barenne's technique of local strychninization. Local stimulation of the visual area on the medial surface of the hemisphere elicited particularly strong "strychnine-spikes" on the lateral geniculate nucleus, together with some activity in the pulvinar and superior colliculus, stimulation of the visual area on the lateral aspect of the hemisphere causing activity in the superior colliculus. Jasper, Ajmone-Marsan and Stoll 1952, stimulating the cortex electrically, found evidence of cortico-fugal projection on to the lateral geniculate nucleus, such

patterns and movement", Hubel and Wiesel 1961, 1962.

effects being obtained from both striate and parastriate areas.

Hubel and Wiesel 1961 compare the organization of receptive fields in the retina, geniculate and striate cortex, and draw attention to the similarities evident; the mutually antagonistic central and peripheral fields, the summation which occurs over regions of the same type, and antagonism between opposing types, and the weaker responses elicited by diffuse light in contrast to those elicited by a suitably chosen restricted stimulus. Subtler differences do, however, exist. In the spatial arrangement of its fields, the geniculate neurones have more in common with the retinal ganglion cells than with striate cortex, the latter having a much greater variety of receptive fields, in contrast to the concentric, circularly symmetrical patterns found in the former. Binocular interaction, if present, would seem minimal at the geniculate level, whereas the majority of cortical cells are so influenced. With diffuse light stimuli the cortical cells are even less responsive than the geniculate neurones and retinal ganglion cells. "Thus at progressively higher levels in the visual system, the cells seem to become less and less concerned with registering changes in total illumination, and perhaps more with the discrimination of complex patterns and movement", Hubel and Wiesel 1961, 1962.

5. Sub-Cortical Visual Activity in the Rabbit.

(i) The Eye.

The orbit opens laterally, making an angle of 85° with the sagittal plane of the head. The apices of the orbits abut each other in the region of the optic foramina and, being shallow, make the eyes protrude, giving the rabbit an extensive field of monocular vision, Sheppard 1961. Duke Elder 1958 determines the alpha angle, measuring the deviation between the optic axis and fixation axis, to be 85° and the visual field for each eye to be 190° in the horizontal plane. The anterior and posterior 10° fields of each eye constitute the fields of binocular overlap. Thompson, Woolsey and Talbot 1950 observe that, though the rabbit's eye seems to swivel through only 20° as gaze is shifted to cover the whole angular field, it would be adequate to give the rabbit an extensive binocular coverage of the nearward field - perhaps of great survival value to it because of the animal's habit of concealment by immobility. This nearward binocular coverage could, however, not be stereoptic because the corresponding cortical areas are not superimposed. From their studies of the representation of the visual field on the cortex, they infer that when each eye converges through 20° the rabbit has an anterior binocular field of 40° , and that the

upper visual field is represented to about 15° above the horizontal meridian and the lower field to "more than 20° " from it. Being equipped thus, with a horizontally extensive, though narrow, band shaped field, it is significant that the rabbit can accurately maintain the horizontal meridian of its eyes while the head is moved through 100° in a fore and aft plane - i.e. rotated about a bitemporal axis - Whitteridge 1960 after de Kleijn 1921.

Polyak 1959 quotes Briggs 1685, Morgagni 1719, Valsalva 1740 and Zinn 1754 as having observed the characteristic fan-like arrangement of optic nerve fibers leaving the optic nerve head in the retina. Chievitz 1891 describes the myelinated fiber band as being 2 mm. wide and 7 mm. long, lying between the upper and middle thirds of the retina and extending horizontally across its surface, with the retinal vessels confined to the area of the band. The area centralis retinae is described as a horizontal white stripe 0.5 mm. wide, lying 2-3 mm. below the nerve head and myelinated band and reaching to within 2 mm. of the ora serrata. Slonaker 1897 confirms these observations. Thompson 1953 mapped ophthalmoscopically the width of the myelinated band along its horizontal extent and found it to subtend 6° - 10° in the field. Sheppard 1961 describes a "visual streak", a band shaped area 3-4 mm.

below the disc and myelinated band where all the retinal layers and the choroid underlying it are thickened, the layer of receptors and inner nuclear layer being here twice as thick as in other retinal areas.

(ii) Optic Nerve and Tract.

Thompson 1953, using a silver fitted glass microelectrode, recorded the responses of single fibers of the optic nerve in response to retinal stimulation by restricted spots of light; "on-off" and continuous "on" types of response were found, increased intensity of illumination leading to a shortening of the latency of the response and increased frequency of the spike discharge. In the early experiments, it appeared that single nerve fibers would respond to the activity of photoreceptors situated anywhere in the retina, indicating that the rabbit eye was no more than a simple detector of light - a seemingly absurd situation in an eye where the dioptric mechanism gives a reasonably precise retinal image. This spurious localization was shown to be due to the intraocular scattering of light by the stimulus spot falling on the medullated nerve fiber band. True localization, with receptive fields of 12° - 15° in the field, were obtained with a shortening of latency and increased frequency of spike discharge as the stimulating light spot moved towards the center of the receptive

field. Thompson makes no mention of the regions of the visual field from which these responses were elicited.

The size of the receptive field is estimated as being equivalent to a circular patch on the retina 1 mm. in diameter. Commenting on this relatively large size of receptive field, Thompson considers it unlikely to have been due to aberrations in the optical system of the eye, increasing the effective size of his test spot, nor as being due to the lateral spread of activity in the retina by the dendrites of giant ganglion cells with a terminal spread of 1 mm. Instead, it was believed that the reduction in latency of the responses as the test spot approached the center of the visual field indicated that the large size of the field was due to interconnections between adjacent ganglion cells and other retinal neurones.

The absolute sensitivity to light at the center of a receptive field in the best preparations was 3 log. units less than the sensitivity of the human eye under similar conditions, with a further fall of sensitivity of 2.5 log. units when the stimulus spot lay on the white fibers of the myelinated band.

The optic nerve of the rabbit is believed to contain about 265,000 fibers, most of them myelinated

Bruesch and Arey 1942. Polyak 1959 quotes Pavlow 1900, Berl 1902, Minkowski 1939, and Overbosch 1927 as believing that the superior colliculus receives afferent optic fibers from the contralateral eye only, indicating a complete or nearly complete decussation of nerve fibers at the chiasma; Jefferson 1940 found more than 75% of the nerve fibers crossing into the opposite tract. The phylogenetically older portions of the infranuclear visual system, the anterior accessory optic tract of Bochnek, the posterior accessory optic tract, the transverse peduncular tract of Gudden, and the large celled nucleus of the optic tract have been shown to be present in the rabbit. Pavlow 1900, Loepp 1912, and Jefferson 1940.

Pavlow 1900, Loepp 1912, Brouwer 1927, from their studies of Marchi material after unilateral enucleation in the rabbit, stated that fibers of the optic tract ended in the ventral nucleus of the lateral geniculate. Jefferson 1940, however, finds that the Marchi reaction appears very largely to be limited to bundles of fibers of retinal origin which run through the ventral nucleus on their way to the dorsal nucleus of the geniculate body - the possibility remaining, however, that the unmyelinated fibers ~~in~~ the unmyelinated collaterals of myelinated optic fibers of passage may end in this

nucleus.

In the dorsal geniculate nucleus, however, Jefferson finds much Marchi granulation scattered as a fine dust through the entire nucleus of both crossed and uncrossed sides, not arranged in definite rows or laminae as if along some definite pathway but rather as representing the terminals of the myelinated optic nerve fibers, ending in relation to the cells of the dorsal nucleus. The reaction in the crossed optic fibers appears more dense and widely distributed than the comparable reaction in the uncrossed fibers. The retinal fibers were observed to end everywhere in the crossed nucleus, except in its dorsal pole and its most medial part, while conversely, the retinal fibers end in the dorsal pole and the medial portion of the uncrossed nucleus. This segregation being incomplete, some degree of overlap is seen at the margins of the dorsal and medial parts of each nucleus. Jefferson observes that Nissl studies reveal some evidence of lamination, produced chiefly by the paths of the incoming tract fibers, but its pattern is complex and cannot readily be integrated with the Marchi findings.

The pretectal nucleus is an oval mass of small, rounded or pyramidal cells situated just medial to the pars posterior of the lateral nucleus of the

thalamus; caudally it enlarges and extends ventrally to the medial aspect of the medial geniculate nucleus. The pretectal and the large celled nucleus of the optic tract are in close topographical relation to fibers of the optic tract, Jefferson agreeing with Loepp 1912 and Brouwer 1927 that some optic fibers end in this region.

(iii) The Superior Colliculus.

The superior colliculus has been shown in a variety of animals to have a laminated structure. Cajal 1911, Tsai 1925, Tsang 1937. Six strata are evident, the nomenclature of Tsang being used in their enumeration.

Layer I Stratum zonale - a thin superficial layer consisting of small marginal cells and a number of fine myelinated fibers.

Layer II Stratum griseum superficiale - a much thicker layer consisting of scattered cells, rather smaller than those in the deeper layers.

Layer III Stratum opticum - in this layer run the fibers of the mesencephalic root of the optic tract and a deeper fiber component of cortical origin. The predominant cells are those of medium size.

Layer IV Stratum lemnisci - the fibers composing this layer belong to the lemniscal systems and to the brachium of the superior colliculus; the cells are small and scattered, with a few giant cells among them.

Layer V Stratum album profundum - this layer contains small scattered cells and the efferent fibers of cells situated in the more superficial layers.

Layer VI Stratum griseum centrale - this constitutes the grey matter surrounding the aqueduct of Sylvius.

It is generally recognized that only the more superficial layers of the colliculus are concerned with the reception of optic fibers. Cajal described the fibers of the mesencephalic root of the optic tract passing first in the superficial layer of the stratum opticum; some fibers terminate here and constitute the "arborisations inferieures", the other fibers continuing obliquely or sinuously towards the periphery of the colliculus, to end at varying levels of the stratum griseum superficiale, almost to the plane of the stratum zonale; these Cajal termed the "arborisations superieures". In Golgi preparations Cajal demonstrated a rich and complex terminal arborization, especially for those

optic fibers which terminate more superficially; here a single retinal fiber makes synaptic connections with many cells of the stratum griseum superficiale. Cajal was of opinion that no fibers of retinal origin turned down into the deeper layers of the colliculus, to end in them, and that no optic fibers ended in the stratum zonale. Loepp 1912, Brouwer and Zeeman 1925, Overbosch 1927 and Jefferson 1940 have followed degenerating retinal fibers in the rabbit to the stratum opticum and the stratum griseum superficiale, none being evident in the stratum zonale. In the cat, Cajal observed that after enucleation of one eye Marchi granulation was limited strictly to the superficial fibers of the stratum opticum, and advanced the view that the fibers of the inferior component were of cortical origin, demonstrating that they ended partly in the stratum opticum itself but largely by turning downwards into the stratum lemnisci.

Hamdi 1953 studied the activity of the superior colliculus in rabbits anaesthetized with urethane or a mixture of "Nembutal" (Pentobarbitone Sodium) and ether, recording the evoked potentials through hand ground steel needle electrodes, of approximately 5 microns tip diameter, in response to a light source subtending 0.25° at the eye. In his series of 23 animals, he notes that 2 animals were in good

condition, though no evidence of localization could be elicited from their colliculi.

The composite results of several experiments enabled him to establish the positions of the meridians of the field on the collicular surface and the fact that the central area of acute vision was relatively well represented, this being also increased along its horizontal extent in contrast to the vertical. Hamdi observes that the surface responses of the colliculus were all well localized in the visual field; the receptive fields, subtending 2° - 5° at the eye, were oval or circular in shape, with response latencies of about 30 m.sec. All responses were derived from the contralateral eye only. Exploring the deeper layers of the colliculus, he finds the localization represented therein closely related to that of the surface, for the position of the receptive fields changes, but by very little, as the recording electrode penetrates the colliculus. The shape and size of the fields, and the amplitude of the responses, however, undergo considerable change. Hamdi observes that, in contrast to the simple round or oval fields obtained from the collicular surface, the fields obtained from the cells of the stratum griseum superficiale and stratum opticum were more complex. In addition to simple field shapes, he finds here

sector shaped fields, with the apex of the sector pointing towards the fixation point, and fields in the form of narrow or broad arcs, concentric about the fixation point, or even more complex fields formed by the combination of fields of these types. In the deeper layers the responses appeared in groups, the short latency responses being elicited only from the central zone of the complex field, the long latency response being evoked from its whole extent, the colliculus beyond the deeper layers of the stratum griseum superficiale yielding only the long latency responses.

The shapes of the fields obtained from the deeper layers, in seven experiments, are recorded. His records of experiments 1, 2, 5, 7 and 11 show predominantly oval fields, subtending up to 30° across their long axis and 10° across the short - all these fields being so situated in the visual field that their long axes lie parallel, or very nearly parallel, to the horizontal meridian. Only Experiment 6, Figures 40-44, reveals oval fields with their long axes lying parallel to the vertical meridian. Experiment 4, Figures 26-33, reveals the more complex field shapes, and even here it is noteworthy that the complex fields can be construed roughly to be oval in shape, with the long axis lying very nearly parallel to the horizontal meridian.

Hamdi's records of receptive fields, obtained from the deeper layers of the goat colliculus, show sector shaped fields; here, too, the long axis of the sectors lie in a plane rotated through 10° - 15° about the horizontal axis.

Hamdi's observations on the rabbit - that the projection of the area centralis retinae on the colliculus shows evidence of increased resolution along the horizontal meridian as opposed to the vertical, and that in the goat and rabbit the receptive fields tended to be, in overall consideration, oval - are significant in view of Chievitz's 1889 and Slonaker's 1897 observations of a band shaped area centralis retinae in the rabbit. Johnson 1901 pictures in the ungulate retina a narrow horizontal band shaped area, devoid of all blood vessels, clearly suggestive of an area of enhanced acuity. This evidence is in sharp contrast with that of Talbot, Woolsey and Thompson 1946 who could find no evidence of a cortical area of greatly enhanced resolution corresponding to that of the fixation point.

II. EXPERIMENTAL METHODS

1. Cat.

Thirty-four cats, weighing 2-3 kgms. each, were used in this series. Anaesthesia was induced slowly, with a "Trilene" (Tri-chlor-ethylene) Air mixture blown into a small glass fronted box containing the cat. When the animal was unconscious it was taken from the box and anaesthesia supplemented with ether from an open mask. Chloralose, 80 mgm./kgm. was made up in 20 cc. of nearly boiling water and a warm solution of this injected slowly into an exposed leg vein. The Chloralose was usually adequate to maintain a desirable level of anaesthesia for 10-12 hours, after which supplementary doses of Chloralose or Pentothal Sodium, 10-15 mgm., intra-muscularly, at half hourly intervals, sufficed to maintain the adequate plane of anaesthesia.

The eyes were flooded with 2% Xylocaine (Lignocaine Hydrochloride) and the lids of each eye approximated with a suture to prevent drying of the cornea during the early stages of preparation. The skull was exposed on the left side through a cruciate skin incision and a roughly circular area of bone, 2 cms. in diameter removed, using a high speed

drill, bleeding from the diploe being arrested with plasticine.

The skin and cartilage of the external auditory meatus were incised to allow easy access to the bony meatus, this being of great help in the correct alignment of the head in the stereo-taxic head holder. The eyes were then reopened and four sutures passed through the limbus at its equatorial and vertical poles, using a fine curved, eyeless ophthalmic needle.

The cat's head was then rigidly fixed between the ear-plugs of a Clarke-Horsley type of stereo-taxic head holder, designed so as not to obstruct the animal's visual field. The head was then levelled about the horizontal plane, and the snout tied on rigidly to the jaw clamp. The skin flaps were raised and their edges sewn on to a lead ring to constitute the walls of a paraffin pool; the dura was then opened and excised under warm oil.

Careful regulation of the body temperature was found to be of the greatest importance. In some of the early experiments accidental overheating led to a rapid deterioration of the animal's condition. In all the later experiments the body temperature was maintained at 38°C by means of an electric blanket regulated by a rectal thermistor.

The head holder was arranged such that the right eye was at the center of a modified Aimark perimeter whose arm had a diameter of 33 cms. The scleral sutures of each eye were tied on to a brass ring such that the slit of the constricted pupil was vertical, these sutures limiting almost completely the spontaneous movement of the eye. A few drops of 1% Atropine Sulphate were now instilled into each eye; this produced full pupillary dilatation which was maintained during the course of the experiment. The attachment of the brass eye rings to the head holder permitted of rotation of the rings, and of their attached eyes, about two planes. When the pupil was fully dilated, the retina was visualized, using a Fison Indirect Binocular Ophthalmoscope, and the eye moved by its ring till the optic disc projected 16° - 18° temporal to the center and 15° - 16° above the horizontal meridian. The central area of the fundus was observed through a mirror placed over the center of the perimeter, and the movements of the eye continued until the area centralis retinae was in view in the center of the ophthalmoscope lens, pupil and perimeter mirror. The area centralis was recognized as a small area of tapetal retina, pale yellow green in colour, towards which blood vessels converged from all directions, but was in itself completely free

of all visible vessels.

When the perimetric projection of the area centralis retinae corresponds to the reference point of the perimeter, the eye is in a position where its visual axis becomes coincident with the axis of reference of the system of spherical polar co-ordinates used to define position in the visual field, this axis now being also parallel to the horizontal plane.

The chief experimental difficulty encountered was the reduction of intra-ocular tension which occurred after a varying interval of time - in the experiments in which only the right eye was fixed, the lowering of tension in this eye was invariably more than in the other. In an effort to minimize this effect a local anaesthetic - Xylocaine - was used to block local pain afferents, and movements of the ring and eye made as minimal and gentle as the conditions allowed.

The perimeter gave white circular patches of light of approximate luminance 1.1 log foot lamberts, i.e. 12.59 foot lamberts, $43.18 \text{ candela/m}^2$, as measured with an S.E.I. Exposure Photometer. Three neutral density filters, reducing the intensity by 1.8 log units in steps of 0.6 log unit, and a circular neutral wedge filter reducing the intensity

by 3.3 log units in steps of 0.1 log unit, could be interposed in the light beam to alter the intensity of the stimulus spot, the diameter of which could be changed from 1. 3, 5 to 10 mm.; the perimeter arm having a radius of 33 cms., the 1 mm. spot subtended 10.4' of arc at the eye. A transistor photo-cell was placed beyond the shutter and its excitation by the stimuli provided synchronization for the cathode ray tube sweep at "on" "off" or "on and off".

Toughened Austenitic Stainless Steel Surgeons' Intestinal needles were electrolytically polished by repeated immersion in a solution made up of:-

Syrupy Phosphoric Acid	42%
Concentrated Sulphuric Acid	34%
Water	24%

6 V. AC. from a mains transformer was passed through the needle and the indifferent electrode, a carbon rod, placed in the electrolytic bath. Satisfactorily polished electrodes had a smooth surface and a long even taper ending in a tip of diameter 1-4 microns. The electrodes were washed in weak alkali and water and dried, and insulated with two or more coats of INSL-X-E 33N clear varnish (The INSL-X Company Inc. N.Y.). The INSL-X was thinned with Chloroform to the consistency of

honey and the shaft of the electrode immersed in it, point upright, until observation through a binocular dissecting microscope showed only the terminal 5 microns standing clear of the varnish. The electrode is then withdrawn slowly from the varnish to ensure coating of the shaft with an even layer of varnish, and allowed to dry, still point upright, in air. After twenty-four hours the electrical resistance of the electrode is measured in a saline bath, using a Heathkit 7 VA Valve-Voltmeter. Measured under these conditions, electrodes with resistances of 350-450 K. ohms gave the best experimental results, both for "mapping" purposes and for extracellular sampling of single units.

The electrode bridge of the stereo-taxic machine carried three micro-manipulators, permitting movement of the electrode in three planes to an accuracy of 10 microns. In the initial experiments, the stereo-taxic co-ordinates given for the geniculate nucleus of the cat - Jasper and Ajmone-Marsan 1954 - were used; in the subsequent experiments the center of the L.G.N. was reached in a plane 6 mm. anterior to the Intra-Aural Plane and 9 mm. lateral to the sagittal suture of the skull.

The activity was displayed by amplification of the voltage between the tip of the micro-electrode

and the indifferent electrode, a silver wire buried in the scalp muscles. A cathode follower and a three stage R.C. coupled amplifier with variable time constant was used, single unit activity being observed and photographed at a time constant of 5 m.sec. The output from the amplifier was fed in parallel to a display oscilloscope, loudspeaker and to the oscilloscopes of a camera unit. A second display oscilloscope carried the signals indicating the "on" and "off" of the stimulus, being activated by the photo-cell of the perimeter. Two double beam cathode ray tubes were included in the photographic unit; the cellular activity, stimulus signal, and a time signal indicating 10 and 100 m.sec. intervals, being carried on three of its traces. For "searching" the visual field, a short duration neon flash was used, this being triggered by the sweep of the display cathode ray tube; exact localization of the receptive field on the perimeter arm, estimation of the field shape, size and threshold, was done with the 1 mm. perimeter spot.

The positions of the eyes were checked repeatedly throughout the experiment, and at its termination, to ensure that no spontaneous or accidental displacement of the visual axes had taken place. At the end of the experiment the cat was killed with an overdose of Nembutal and perfused through

the ascending aorta with 10% buffered formol in normal saline. After twelve hours the brain was removed from the skull and serial parasagittal sections made at 100 microns on a freezing microtome. Frozen parasagittal sections at this thickness gave the best results, shrinkage and distortion during fixing were minimal, and in this plane a considerable extent of each electrode track could be discerned in the appropriate sections.

The serial sections were mounted on slides coated with 0.5% gelatine solution, exposed briefly to formol vapour and dried on a hot plate. The sections were cleaned by washing in ascending grades of alcohol and Xylol, and then through descending grades of alcohol. They were stained for fifteen minutes in 1% Toluidine blue ("Michrome", Edward Gurr); after dehydration in alcohol, they were differentiated in Gotthard's Differentiator and finally cleared in Absolute Alcohol and Xylol and mounted in D.P.X. Mountant (B.D.H.).

Accurate outline drawings of the L.G.N. and of the electrode tracks were made by means of a slide projector which was adjusted to give a linear magnification of 15. Superimposition of the drawings of adjacent track bearing slides gave a reliable method of reconstructing the entire extents of the electrode tracks.

The projection of the "dorsal surface view" of the L.G.N. was made by direct measurement of the extent of nucleus, anterior and posterior to the tracks, and by determining the positions of the anterior and posterior borders of the posterior vertical "curl" in relation to the tracks.

The plane projection of the surface area of lamina A was obtained by measuring the surface length of this lamina on each section and representing each by a strip of paper of appropriate length, and 1.5 mm. width, to correspond to the 100 microns section at a linear magnification of 15.

On each strip the positions of the electrode tracks were marked, and these enabled the adjacent strips to be aligned, one with respect to the next; thus the ends of the strips demarcate a surface area which corresponds to that of the dorsal surface of A at the appropriate magnification. The surface thus constructed represents accurately the surface of the thickened central region of the nucleus, where the nucleus changes shape evenly, and its laminae are well demarcated. The nucleus shrinks rapidly in size towards its lateral pole, and the anterior and posterior ends of the lamina approximate and fuse with each other ventrally, thus making essential a spacing apart of the adjacent strips by

slightly more than 1.5 mm. At the medial pole of the nucleus, all semblance of lamination is lost and its outline difficult to determine with certainty, consequently little more than an approximation of the surface area of this region is possible.

2. Rabbit.

Twenty-four rabbits, each weighing 2-3 kgms., were used. In the earlier experiments they were anaesthetized with Paraldehyde 1 cc./kgm. intramuscularly, followed half an hour later by 3 cc./kgm. of a 25% solution of Urethane injected into an ear vein. In the later experiments 4.0 cc./kgm. of a solution made up of 500 mgm. Chloralose and 5.0 gms. Urethane in 25 cc. of nearly boiling water was given intravenously. This initial dose was usually adequate to maintain the desired level of anaesthesia for 8-10 hours, supplementary doses of Nembutal (0.1 cc. in 1 cc. of 0.9% Saline) being given intravenously or intra-muscularly at half-hourly intervals if the level of anaesthesia lightened.

The skull was exposed on the right side through a cruciate skin incision, and a circular piece of bone removed from the skull overlying the region of

the superior colliculus. The skin and cartilage of the external auditory meatus were incised to allow access into the bony meatus; this greatly facilitates skull fixation in the stereo-taxic head holder, for the external auditory canals of the rabbit pursue a very oblique course between their external and internal meati.

A relatively simple head holder was used, but it provided rigid fixation of the skull in the intra-aural plane without obscuring the extensive field of vision of the laterally placed eye.

The head holder was so arranged that the left eye was at the center of the perimeter, with the sagittal plane of the head at right angles to the axis of reference of the perimeter. The eye was centered on the perimeter by observing on the center of the cornea the image of a small illuminated cross placed at the reference point of the perimeter; the eye in this position has its optic axis coincident with a horizontal axis passing between the center and reference point of the perimeter. In several experiments the Fison Indirect Binocular Ophthalmoscope was used to plot on the perimeter the projection of the optic nerve head and margins of the central part of the myelinated nerve fiber band.

In the early experiments the stereo-taxic co-ordinates of Sawyer, Green and Everett 1954 were used to reach the colliculus. These stereo-taxic co-ordinates define position with reference to the bregma and the midline suture of the skull when the head is fixed in the intra-aural plane such that a horizontal plane passing through the bregma lies 1.5 mm. above the level of the lambda. The colliculus lies within P.10 and P.15 and between 0-5 mm. lateral to the midline. On its way to the colliculus, the electrode records the cellular activity of the grey matter of the dorsal and ventral surfaces of the cortex, and with the electrode tip between the ventral surface of the cortex and the dorsal surface of the colliculus, from the conducting medium. This yields a large polyphasic response which is sharply localized in the visual field; with further downward movement of the electrode the surface layers of the colliculus are reached, this being characterized by an abrupt change in the "quality" of the response; the low pitched sound of the polyphasic response changes to a higher pitched crackle of cells, the equivalent changes being seen in the oscilloscope.

At the end of the experiment the rabbit was killed with an overdose of "Nembutal" and the brain fixed by perfusing the head through the ascending

aorta with 10% buffered formol saline. The brain was then removed and frozen sections made at 100 microns, being stained subsequently with Toluidine blue.

Retinal ganglion cell counts were made in isolated eyes, the plane of orientation of which had been established during life. In the cat, the slit of the constricted pupil established an almost vertical plane and the cornea was scored along it with a small cautery; in the rabbit, the cornea was scored along a plane parallel to the myelinated nerve fiber band. These animals were then perfused through the aortae with Kolmer's fixing solution. After fixation, the isolated eyes were embedded in paraffin and the lenses removed. The eyes were sectioned at 10 microns, vertical sections being made in the cat and horizontal in the rabbit, and stained in cresyl fast violet. Retinal ganglion cell counts made in these sections were checked against those made at right angles to the plane of the original sections to ensure that no gross errors, due to distortion or shrinkage, had occurred.

III. EXPERIMENTAL RESULTS

1. Cat.

(i) Morphology of the Lateral Geniculate Nucleus.

The laminar pattern - of a total of 247 electrode penetrations into the nucleus, 198 were into its central region; these tracks, passing successively through laminae A, A₁, B, recorded evoked responses from the contra-lateral, ipsi-lateral and contra-lateral eye respectively. 6 electrode tracks were in the extreme lateral pole of the nucleus and recorded responses from the contra-lateral eye only; here the histology shows lamina A, its anterior and posterior ends, approximating each other ventrally, with a small central core of cells which represents the lateral extent of lamina B. 23 stabs were in the posterior region of the nucleus. Here the parasagittal sections reveal an almost vertical plate of cells, composed predominantly of laminae A and A₁; B being greatly reduced or non-existent. The vertical plate of cells is bent on itself in a vertical plane to form, in section, a C shaped structure, with its concavity facing anteriorly and bent again about a transverse plane, giving the posterior margin of the nucleus a gently C shaped curve, again concave anteriorly.

The laminae are arranged with A anteriorly and A₁ behind it, but usually a small extent of the upper extent of A bends back over the vertical crest to lie on the posterior surface of the vertical plate. Much more rarely this terminal extent of lamina A bends anteriorly - Figure 4. The fibers of the optic radiation emerge from the anterior surface of this posterior curl and pass forwards and upwards to reach the cortex, these fibers filling in the anterior concavity formed by the curvature of the posterior curl. The vertical extent of the posterior curl is maximal about its mid-region, falling off rapidly towards the lateral pole of the nucleus and much more gradually towards its medial limit. The size and extent of curvature of the posterior region shows considerable variation between individual nucleii; in some the curvature is minimal, the laminae being vertical in their orientation; in other nucleii the laminae form a prominent curve in one or both planes.

The disposition of the laminae in such a manner make the records obtained during the transit of the electrode through these laminae confusing, and makes subsequent co-relation of the electrical records with the histology essential. Thus, an electrode passing vertically through the posterior curl may encounter successively lamina A, optic

radiation, A, A₁ and B - e.g. Figure 5; more posteriorly an electrode would traverse A₁, A, radiation, A, A₁, B or A₁, A, A₁, B or B, A₁, A, A₁, B - e.g. Figure 5. When the curvature of the laminae is minimal, the electrode passes vertically down along the length of the laminae; thus an anteriorly placed electrode would traverse the length of A and then pass into A₁ and B - e.g. Figure 7; more posteriorly an electrode would traverse the vertical extent of A₁ before passing into B, yet more posteriorly an electrode would record briefly from B.

In the postero-medial region, the nucleus shrinks rapidly in size and is represented by a medial extension of the posterior vertical curl - the Nucleus Interlaminaris Medialis of Thuma. Here too, the vertical plate of cells is curved in two planes, vertical and transverse, presenting an anteriorly directed concavity. In parasagittal section, e.g. Figure 8, the anterior surface is seen to be of irregular outline, cell groups of varying size being found detached from the nucleus and scattered among the fibers of the optic radiation.

Transverse sections - Figures 9, 10 - show a shallow groove demarcating the main mass of the pars-dorsalis from this medial cell group. The laminae, characteristic of the pars-dorsalis,

terminate abruptly at its medial edge; none are seen in the medial extension. The cell density of the pars-dorsalis is also significantly higher than that in the medial extension, though the same cell types - principal, small and large - are found irregularly scattered, in the same numerical proportions as in the more lateral pars-dorsalis. When serial parasagittal sections are examined, the main nuclear mass merges into its medial extension without obvious differentiation; more medially still, the medial extension thins out antero-posteriorly and merges imperceptibly with the pulvinar. The dimensions of this extension vary considerably between animals, and its determination is made even more difficult by the fact that, being sparsely cellular, its outline is more difficult to delineate from the adjacent thalamic nucleii and from the optic radiation. Its vertical extent is 3.5-4.0 mm. and is its most constant dimension; its antero-posterior width 0.5-1.5 mm., and transverse extent 1.0-2.5 mm. from the medial border of the pars-dorsalis.

A sagittal section through the middle of the pars-dorsalis reveals the trilaminar pattern at its most obvious, e.g. Figure 4. The two dorsal laminae A and A₁ seem identical in size and structure; anteriorly, where the laminae are horizontal, each

is of almost uniform thickness, being here about 0.5 mm.; posteriorly, where the laminae are nearly vertical, each shrinks to about 0.25 mm., the laminae thinning out progressively as they reach their terminal extents. The density of cells in these laminae remain uniform throughout their extents; where the laminae are thickest, the cells are packed 20-25 deep, and in the thinned out posterior regions 10-12 deep.

Within each of these two laminae, Toluidine blue stained sections show no evidence whatsoever of an intra-laminar segregation of cells, either into clusters of "glomeruli", into sub-laminae, or into radial rows along the terminal branches of the optic tract afferents. The interlaminar fiber plexus AA₁ separates the laminae throughout their extents, except in their anterior, lateral and ventral extremities where the two laminae tend to fuse with one another, obscuring the interlaminar plexus. The AA₁ fiber plexus itself is very sparsely cellular - the majority of the cells present in the interstices of the plexus are small, being 5-10 microns in diameter; irregularly scattered amongst these are a few large, deeply staining cells about 25 microns diameter. These cells constitute the Nucleus Interlaminaris Centralis of Thuma and are most frequent in the regions

where the laminae are horizontal and thickest.

The A_1B interlaminar plexus separates the laminae A_1 from B, but it is much less obvious than the AA_1 plexus, both because the former is more cellular and because the layer B is itself greatly thinned out posteriorly. Anteriorly the layer B is thicker than either A or A_1 , being here nearly 0.75-0.85 mm. in thickness; at the base of the posterior curl it is reduced to about 0.35 mm.; beyond it thins out even more rapidly and can only rarely be made out as a separate layer for it lies closely applied to the posterior surface of A_1 , the intervening fiber plexus A_1B being either insignificant or absent. Electrophysiological evidence for a layer B in this region is, however, provided by an electrode yielding contralateral eye responses.

The A_1B plexus, too, is populated by irregularly scattered small cells and a smaller number of large deeply staining cells. In the anterior part of the nucleus, where layer B reaches its greatest thickness, these large cells are most numerous; in some sections they are seen to accumulate in sufficient numbers to form a small horizontal plate of cells, lending justification to Rioch's claim for a "lamina magnocellularis".

Anteriorly, the Nucleus Perigeniculatus Anterior

forms a thin layer of cells lying over the dorsal and antero-inferior surface of the pars-dorsalis and is separated from it by a layer of fibers. Antero-inferiorly this layer of small cells becomes confluent with the pars-ventralis of the lateral geniculate body. Postero-inferiorly these small cells constitute the Nucleus Perigeniculatus Posterior, which is closely applied to the postero-ventral surface of lamina and from which it cannot be readily differentiated.

(ii) Single Unit Activity.

In the course of this study, the activity of 162 single units was observed; this total being made up of 67 units from A, 29 from A₁, 37 from B and 29 from the Anterior Perigeniculate Nucleus.

Activity in A and A₁.

Of the 67 units from layer A, 47 gave center "on" responses and 20 center "off". Multiunit responses suggested that the cells yielding center "on" responses were aggregated in the upper, i.e. dorsal, aspects of laminae A and A₁, whereas cells yielding center "off" responses were located in the lower, i.e. ventral, parts of the laminae. These 67 A units were hence analysed with respect to the position of their cells in the lamina by

comparison of the depths at which the electrode tip just entered and left a lamina with the depth at which the responses were observed during the course of any single electrode penetration, cells lying in the upper half of the thickness of the lamina being considered "in the upper layers".

Total Center "on" units in lamina A - 47

3 from "deeper layers" of lamina A

3 from posterior vertical extent of lamina A

41 from "upper layers" of lamina A

These figures show a well marked tendency for the cells yielding center "on" responses to be aggregated in the upper aspects of the lamina.

In the vertical posterior curl the electrode travels along the length of a lamina rather than across its width, hence the position of a cell within the thickness of the lamina cannot be determined with certainty. Three cells from the deeper aspect of A yielded "on" responses; this may indicate that the segregation of "ons" and "offs" is not an absolute one, else that the "on" responses were not true "on" center responses but "on" responses from the periphery of a true "off" center field.

Total Center "off" units in lamina A - 20

2 from posterior vertical extent of lamina A

18 from "deeper layers of lamina A".

The 29 units in lamina A_1 have a similar distribution.

Total Center "on" units in lamina A_1 - 19

18 from "upper layers of lamina"

1 from the posterior vertical part.

Total Center "off" units in A_1 - 10

8 from deeper layers of A_1

2 from the posterior vertical part.

All the units studied behaved in the manner described by Kuffler 1953, i.e. they were either center "on" types with a peripheral "off" surround, or center "off" types with a peripheral "on" surround. The central and peripheral fields show mutually antagonistic actions; whereas increase of stimulus size up to the size of its own receptive field or increase of intensity of stimulus produces summation effects, Figure 12, records J_1 and J_2 show summation effects being expressed as a reduction in the latency of a short center "on" type of response. Figure 12 K_1 shows response of a center "off" unit produced by a 1 mm. spot; K_2 shows the response of the same unit when the 1 mm. spot is replaced by a 5 mm. spot; the "off" response is now greatly diminished, simultaneous stimulation of a part of the peripheral "on" field causing

peripheral inhibition of the center "off" response.

Figure 12 L_1 shows continuous "off" center activity from units in layer B. Increase in level of background illumination, i.e. increase in stimulus intensity of the peripheral "on" field, causes inhibition of the center "off" activity in L_2 . Further increase of background illumination, L_3 , causes further summation of the peripheral "on" effects, resulting in marked peripheral inhibition of the center "off" response.

Some "on" and "off" center units respond with a short burst of action potentials when stimulated appropriately - the "on" centers yield a short burst only at the commencement of the stimulation, prolonged illumination producing no further response, e.g. Figure 11 A; comparably the "off" centers with a brief burst of activity at the cessation of illumination, e.g. Figure 11 H. Other units, however, show continued activity, lasting as long as the appropriate stimulus is maintained, e.g. Figure 11 B, C, F, and I. All units responding in this manner show adaptation, the initial frequency of the action potentials diminishing with the duration of stimulation. It is uncertain whether the "short" burst types and the "continued" effects types constitute two functionally different types, whether the short burst types could be made to

respond continuously in response to more complex patterns of stimulation, whether they reflect differences in the rapidity of adaptation, or whether the short burst types are merely the responses to sub-maximal stimulation of their receptive fields. The units studied showed no correlation between their behaviour in this sense and the positions of the cells in the thickness of the lamina.

The size of the central receptive field was measured in 34 units in laminae A and A₁.

8	had	central	fields	1°-2°	in	diameter
18	"	"	"	3°-4°	"	"
7	"	"	"	4°-6°	"	"
1	had	a	field	of	over	8° across.

All eight units with small receptive fields were obtained from positions in the nucleus corresponding to visual field points within 10° of the center, and all but one of the seven units with fields of 4°-6° had localizations in the visual field beyond 25° of the center. It is likely that the true size of the receptive fields measured are smaller than indicated for these determinations have been made on atropinized eyes; the absence of any accommodation making it unlikely that the test spots at a distance of 33 cms. from the eye could be focussed sharply on to the retina. Even so

it is probable that the steel electrodes used have sampled only the larger geniculate cells, for it is likely that electrode size, cell size and measured receptive field size are related. Thus Wiesel 1960, using platinum microelectrodes and recording from the retinal ganglion cells, could find no receptive fields smaller than 2° , whereas capillary micropipettes with very fine tips recorded receptive fields of 0.5° .

Thresholds were estimated in 31 units in laminae A and A_1 ; the 1 mm. spot was used, neutral density filters being added on to reduce the intensity of the stimulus until a response was no longer obtained, the threshold being expressed in terms of the density of the filter required to elicit a minimal response.

Total number of units sampled - 31

- 3 yielded minimal response to 1 mm. spot with 0.6 log unit
- 11 yielded minimal response to 1 mm. spot with 1.2 log units
- 8 yielded minimal response to 1 mm. spot with 1.8 log units
- 4 yielded minimal response to 1 mm. spot with 2.4 log units
- 5 yielded minimal response to 1 mm. spot with 3.0 log units.

These being composite results derived from several different experiments can yield no more than an

approximation, for, in addition to a bias introduced by sampling of the larger cells, significant variations are introduced by differences in the levels of dark adaptation and by the general condition of the different animals, especially with respect to the state of their retinal circulations.

Cell Activity in Lamina B.

35 single units were observed in lamina B, 11 of these were center "on" types and 24 center "offs", there being no evidence of a segregation of these cells into upper and lower aspects of the lamina as occurs in A and A₁. In lamina B, too, some units respond with brief bursts at "on" or "off" - e.g. Figure 11 H, others with continuous activity during the period of stimulation - e.g. Figure 11 F, I. The center "off" activity of B units appears significantly different from those in A and A₁ in this respect, for of the total of 24 center "off" units sampled 20 showed continuous activity in the dark, only 4 showing brief "off" activity.

The size of the receptive field centers were determined in 21 units, 10 of them had centers up to 5° diameter and 11 had centers over 10° across. It was found to be much more difficult to determine with any consistency the size of the peripheral

fields, for some of these units were of very low threshold and extremely sensitive to very low intensities of stray background light and consequently even more dependent on the level of dark adaptation reached at the time of determination of thresholds and field size.

The threshold sensitivity was measured for 14 units:-

2 units responded to the 1 mm. spot with 1.2 log unit filter.

7 units responded to the 1 mm. spot with 3.0 log unit filter.

3 units responded to the 10mm. spot with 4.7 log unit filter, i.e. equivalent to 1 mm. spot with 2.7 log unit filter.

2 units had very low thresholds, almost equal to that of the fully dark adapted eye of the observers.

The activity of cells in lamina B seems different to those of A and A_1 in many respects; by virtue of the absence of segregation of "on" and "off" center units, the greater proportion of "off" units to "on" units, the greater proportion of continued "off" with respect to short "off" effects, and the greater proportions of units with larger receptive fields and lower thresholds. Several units in B showed great sensitivity to the level of background illumination, Figure 12 L_1 , L_2 , L_3 , this feature being a manifestation of their very

thresholds, or the very large size of their peripheral receptive fields, or both. It was also frequently observed that the size of a center "off" response depended on the size and intensity of the stimulus and the duration of the period during which the unit was inhibited by the presence of the stimulus. Large or intense stimuli, or prolonged illumination diminished the size of the "off" response obtained when the stimulus was discontinued; the continuous "off" response then becomes slowly larger over a period of several seconds in a manner very suggestive of light and subsequent dark adaptation, though with a much more rapid time course; 3 hours being required for complete dark adaptation in the cat. The sensitivity of cells in B to small doses of Nembutal (Sodium Pento-barbitone) was observed in the course of two experiments where 0.2 cc. were injected intramuscularly to supplement the Chloralose anaesthesia, while the recording electrode was in layer B - the Nembutal produces a marked diminution of the resting background "dark-discharge".

Perigeniculate Cell Activity.

29 single units were obtained from this layer of cells, responding in a very characteristic manner. A flash of short duration produces a high frequency

burst of action potentials lasting for about 0.2 sec. The burst shows an initial spike frequency of over 600/sec., adapting rapidly to about 100/sec. - Figure 11 D. Of the 29 units, 25 could be activated by illumination of either eye from very large central receptive fields usually 20° - 40° across.

Lamina Magnocellularis Cell Activity.

2 units were observed in this lamina. These units could be activated independently from either eye by a single stimulus in the visual field; a small electrolytic lesion made after recording the activity from one of these cells enabled subsequent identification of the position of the electrode tip.

(iii) Retino-topic Projection on the Lateral Geniculate Nucleus.

When the visual axes of the two eyes are made coincident with the axis of reference of the system of spherical perimetric polar co-ordinates, an electrode passing vertically through a lamina, and successively through laminae A, A_1 , B, records from units whose receptive fields are related to each other in a consistent and orderly manner, laminae A and B responding to stimulation of the contralateral eye, while A_1 responds to stimulation of the ipsilateral eye.

In the anterior and central region of the nucleus, where the laminae are nearly horizontal, an electrode passes through them very nearly normal to their surfaces; the changes in position of the receptive field are consequently minimal, a single stimulus position or a small area in the visual field yielding responses as the electrode traverses the successive laminae. Elsewhere in the nucleus the curvature of the laminae make for an oblique course of the electrode through them, giving rise to greater displacements of the visual field localizations yet preserving within each lamina, and between adjacent laminae, a consistent and orderly pattern of change.

In Figure 13 the points of entry of the electrode into the surface of lamina A are denoted, while in the visual field are drawn the successive changes in localization produced as the electrode passes through the thickness of the lamina.

Electrode positions 1-7 produce localizations in the upper peripheral field, with subsequent displacements towards the center as the electrode travels down for a relatively great length along the vertical extent of the lamina.

Positions 9-13 on the lateral aspect of the nucleus yield localizations around the periphery

of the horizontal meridian. The passage of the electrode produces considerable displacement of the field points, further peripherally, both because the electrode passing obliquely through the lamina traverses a considerable thickness of it and because a relatively large extent of the peripheral visual field is represented in this limited region of the nucleus.

Similarly positions 14, 17 and 20 in the anterior pole of the nucleus yield localizations in the lower field, with considerable displacements of these points further peripherally, corresponding to the passage of the electrode through the lamina.

In marked contrast to these, positions 15, 16, 18 and 19 in the anterior and central regions of the nucleus correspond to receptive fields in the central visual field, with minimal subsequent displacements because here the electrode passes in normal to the surface of the lamina and because of the considerable extent of the lamina devoted to the representation of a small area of the central visual field.

In the subsequent experiments, the visual field localizations corresponding to points on the dorsal and anterior surfaces of the pars-dorsalis were obtained and these results used to determine

the projection of the meridians and of the semi-circles of equi-angular deviation of the right visual hemi-field on the surface of lamina A of the left pars-dorsalis.

The results of 7 such experiments are reproduced - Experiment C₂₀ Figure 14, Experiment C₂₃ Figure 15, Experiment C₂₈ Figure 16, Experiment C₂₄ Figure 17, Experiment C₂₉ Figure 18, Experiment C₃₃ Figure 20, and Experiment C₃₄ Figure 21.

These results confirm the evidence obtained by earlier workers using histological and electrophysiological techniques, for it is apparent that the central part of the Right Visual Hemi-Field is projected on the medial aspect of the left nucleus, the lower field quadrant on its dorsal and antero-inferior aspect, while the upper field quadrant is represented on the anterior surface of the posterior vertical curl.

The central field is represented on a disproportionately large extent of the nuclear surface, the peripheral visual field being consequently represented along a narrow border chiefly on the lateral and antero-lateral aspect of the nucleus.

The projections of the meridians of the visual hemi-field radiate outwards from the medial aspect of the nucleus; the upper vertical meridian - i.e.

0° - 90° , runs directly backwards along the anterior surface of the posterior curl, the lower vertical meridian i.e. 0° - 270° , directly forwards and downwards to the antero-inferior aspect of the nucleus, with the horizontal meridian - i.e. 0° - 180° , running antero-laterally across the surface of the nucleus, lying first almost at the base of the posterior vertical curl then deviating forward as the periphery of the meridian approaches the lateral pole. The meridians of the upper field quadrant, lying between 0° - 90° and 0° - 180° , are consequently confined to the region of the posterior curl. The vertical runs directly posterior, the succeeding ones run obliquely, each one moving progressively more lateral as they approach the direction of the horizontal meridian. The lower field quadrant has its meridians spread across the anterior convex surface of the nucleus; these run obliquely in an antero-lateral direction, becoming progressively more anterior till the lower vertical meridian is reached.

The semi-circles of equi-angular deviation of the visual hemi-field are projected on the surface of the nucleus in a more complicated fashion, these undergoing more distortion in the course of their projection than do the meridians. Each semi-circle of the field seems to undergo unequal distortion

about its segments in the upper and lower quadrants, the distortion of the segment of the lower quadrant being considerably more than of its upper half.

Hence, the projection of each semi-circle of field seems to consist essentially of two arcs corresponding to the upper and lower quadrants of fields, the arc of the upper quadrant being that of a circle of small radius, whereas the arc of the lower field is that of a larger circle. The experimental results reveal that the actual distortion of these semi-circles is perhaps even more complicated than if visualized as a simple difference between upper and lower fields, for the arcs contained between the meridians 180° - 240° seem to show an even greater extent of distortion than that which holds for the rest of the lower field. Thus the projection of the part of the semi-circle in this region becomes almost ellipsoid, the extent of distortion becoming rapidly diminished towards the upper quadrant projection and less rapidly diminished in the projection of the rest of the lower field quadrant.

The areas of surface enclosed by the 10° and 20° semi-circles indicate quantitatively the disproportionately large representation of the central visual field. Thus the 10° semi-circle occupies almost one-third of the available surface, while the 20° semi-circle almost half, and correspondingly

the peripheral field is projected on a narrow rim of surface on the posterior, lateral and antero-inferior aspects of the nucleus.

The convexity of the lateral and dorsal surfaces of the nucleus conceals from dorsal view the disposition of the projection of the peripheral field, while the vertical alignment of the posterior curl conceals completely its anterior surface and hence the projection of the upper field quadrant.

In an attempt to overcome these difficulties an effort was made to project the surface of lamina A on a plane surface by aligning together several strips of paper of appropriate width, the length of each of which corresponds to the length of the lamina in appropriate parasagittal sections. The surface area thus constituted represents accurately the dimensions of the large central region of the nucleus and the antero-posterior dimensions of the entire lamina, but represents with some distortion the transverse dimensions of the lateral and medial poles where the nucleus has a very markedly convex surface.

The plane projections of the surface so constructed illustrate the results of 4 experiments - C₂₄ Figure 17, C₂₉ Figure 18, C₃₃ Figure 20, and C₃₄ Figure 21.

The results of experiments C_{24} and C_{29} demonstrate the general disposition of the central visual field, C_{33} the projection of the peripheral field on the lateral aspect of the nucleus, and C_{34} the projection of the upper field on the anterior surface of the posterior vertical curl.

These diagrams make more apparent the characteristic features of the projection of the visual field on the L.G.N. The increased distortion of the arcs of the lower field with respect to those of the upper field, and the even greater distortion of the arcs lying between the 180° - 240° meridians, make the projection of the horizontal meridian divide the surface of lamina A into two unequal areas, the lower half field being represented on an area considerably larger than that which represents the upper field.

(iv) Magnification Factors for Upper and Lower Field Quadrants.

The variations of the magnification factor with retinal eccentricity were determined in several experiments, the results of 6 experiments being reproduced - Experiment C_{15} Figure 22, Experiment C_{20} Figure 23, Experiment C_{21} Figure 24, Experiment C_{24} Figure 25, Experiment C_{29} Figure 26, and Experiment C_{33} Figure 27, and the composite results of all

these experiments together in Figure 28.

These results produce quantitative evidence for the observation that the central field receives a relatively large surface of representation; the central field receives nearly 0.6 mm. of surface per degree, whereas peripherally the value falls to 0.02 mm./degree, a linear ratio of nearly 30:1.

When plotted separately, the magnification factors obtained from field points in the upper field quadrant differ significantly from those of the lower quadrant, these points constituting a curve with consistently lower values. The curve obtained for lower field positions show, in addition to the consistently higher values, a considerable scatter of points. Comparison of these curves with the maps of surface projections make evident the fact that the scatter is due to the unequal distortion of the lower field arcs, especially of those lying on the antero-lateral aspect of the nucleus wherein are represented the 180° - 240° meridians.

(v) The Extent of the Visual Field.

All the peripheral limits of the visual hemi-field have not been obtained during the course of any single experiment, yet the composite results

of all permit of a reasonable estimate, for even though some small differences do exist between the alignments of the fixation axes in different experiments, the peripheral localizations reflect these differences to a much smaller extent because the areas of nuclear surface devoted to the representation of these fields are relatively small.

For the left nucleus localizations have been obtained from the right eye, 40° above and 60° below fixation point on the vertical meridian, and from 90° temporal to the fixation point on the horizontal meridian. When these values are plotted on the plane surface projection of the lamina, it is evident that some small areas of nuclear surface, peripheral even to these values, are still available, particularly in the region of the lower vertical meridian, thus making it likely that the lower vertical meridian is represented up to at least 80° .

The lamina A_1 of the left nucleus receives the projection of the right hemi-field of the left eye; from its extreme lateral extent localizations have been obtained corresponding to field positions 70° temporal to the fixation point on the horizontal meridian, thus indicating the extent of the overlap of the visual fields of the two eyes.

(vi) The II^{ry} Visual Area.

The results of Experiment C₃₄ Figure 21 demonstrate the fact that when the electrode position moves progressively medial along the upper surface of the posterior vertical curl, the corresponding localizations in the field move centrally along the meridians of the upper field quadrants until the upper vertical meridian, 0°-90°, is reached. Figure 30 illustrates the results obtained in 5 experiments where the electrode passed progressively more medial, and antero-medial, to record from the Nucleus Interlaminaris Medialis. In these electrode positions, the field localizations begin to move away from the vertical meridian and progress towards the horizontal meridian. These results strongly suggest that the visual hemi-field is represented in this narrow postero-medial extension of the pars-dorsalis as a diminutive mirror image of that projected on the main nucleus. The results illustrated in Figure 30 represent only the localizations obtained from the upper surface of this vertical plate of cells; as the electrode passes through it the field localizations change in a consistent manner, though at a faster rate, being indicative of the smaller scale at which the mirror image is represented. Yet, however, the construction of a projection map of the mirror image,

comparable to that of the I^{ry} area, is one of considerable difficulty. The entire transverse extent of this region is not more than 2.5 mm., often considerably less, and its curvature about the vertical and horizontal planes makes the greater extent of its anterior surface inaccessible to an electrode passing down in a vertical plane. The histological features of this region make the difficulties of establishing projection lines even greater. Hayhow 1958, described the medial interlaminar nucleus as consisting of three poorly defined approximately vertically orientated bars of cells, but concluded that a careful comparison of the disposition of the ipsilateral and contralateral eye connections in this area indicated that the existence of a considerable overlap between them was highly likely, for the diffuseness of the region precluded the accurate designation of either specific ipsilateral and contralateral areas of terminal arborization or of the extent of the zone of overlap between them.

(vii) Retinal Ganglion Cell Concentrations.

Ganglion cell counts were made to determine the relationship between their distribution in the retina and the pattern of projection of the visual field on the geniculate nucleus.

The results obtained from one eye are illustrated - Figure 29.

The counts were made from vertical sections of the retina, 10 microns thick. A series of sections passing through the optic nerve head and the area centralis were chosen and the counts made in five sections, each of these being separated by 450 microns from the adjacent section; the total counts were representative of a vertical strip of retina 1850 microns wide. In each of the chosen sections, the extent of the retina was divided into segments, each measuring 745 microns, and the number of ganglion cells in each of these segments determined, noting also in each segment, where they occurred, the presence of the ora serrata, tapetum or optic nerve head.

Strips of paper, containing the relevant details of each segment, then represent each of the five chosen sections, and these can be aligned, enabling the positions of the ora serrata, tapetum and optic disc to be determined on this strip of retina. In Figure 29 the column of figures on the left indicates the sum of the ganglion cells in the corresponding 745 micron segments of the five sections at each horizontal level. Lines are drawn linking up areas with equal ganglion cell counts, and these "contour" lines of ganglion cell

concentrations then demarcate the position of the area centralis which lies about 3.5 mm. temporal to the center of the optic disc and slightly above the level of a horizontal plane, passing through the disc. In this vertical strip of retina, the tapetum extends for nearly two-thirds of the extent of the retina, between the upper and lower margins of the ora serrata, thus lying across the entire upper half of the retina and across part of the lower - the optic disc and area centralis thus lie within the tapetal retina.

10 The high ganglion cell concentration of the area centralis, with gradual diminution of the counts towards the peripheral retina, corresponds to the shape of the magnification factor curve and explains the disproportionate representation of the central and peripheral visual fields on the surface of the L.G.N. The disparity of areas devoted to the upper and lower field quadrants do not, however, seem to have these differences reflected in the ganglion cell concentrations of upper and lower retinal halves, for these cell counts seem to fall off equally in both directions along a vertical plane passing through the area centralis - Figure 29.

2. Rabbit.

(i) Projection of the Visual Field on the Surface of the Superior Colliculus.

The projection of the visual field of the left eye on the surface of the right superior colliculus was determined with the left eye at the center of the perimeter arm, such that a horizontal axis passed through the reference point of the perimetric co-ordinates and the center of the eye of the anaesthetized rabbit.

The projection of the field was determined in 10 experiments, the results of 5 of which are reproduced - Experiment R₃ Figure 33, Experiment R₇ Figure 34, Experiment R₁₇ Figure 35, Experiment R₁₈ Figure 36, and Experiment R₁₉ Figure 37.

These results establish clearly that the visual field represented on the collicular surface, with the eye of the anaesthetized animal in this position, is in the shape of a narrow band, for though extending through almost 180° in the horizontal plane, it has a maximal vertical extent of not more than 40° - 50° . The maps establish, too, that the band shaped field is tilted, such that the peripheral extent of the posterior field lies confined between the 0° - 30° meridians, and correspondingly the periphery of the anterior field lies below the horizontal meridian, extending into the

lower field as far as the 220° meridian.

The horizontal extent of the band shaped field is represented along the antero-posterior axis of the colliculus, with the anterior (i.e. nasal) field projected anteriorly and the posterior (i.e. temporal) field projected posteriorly. The short extent of the vertical meridian included within the visual field is represented along the transverse axis of the colliculus, the upper vertical meridian, i.e. 0° - 90° , medially and the lower vertical, i.e. 0° - 270° , meridian laterally. Differences in the position of the eye between individual experiments make relatively little difference to the extent of the horizontal field represented or to the tilt of the band, the chief variation between experiments being in the relative amounts of upper and lower field represented. Thus in Experiment R_{18} Figure 36, the upper and lower fields are represented to almost equal extents, in Experiments R_{19} Figure 37 and Experiment R_3 Figure 33 the lower field representation is increased at the expense of the upper field, whereas in Experiment R_7 Figure 34 and Experiment R_{17} Figure 35 the band lies almost entirely across the lower field.

The antero-posterior and transverse diameters of the colliculus are roughly comparable, yet on

its antero-posterior axis are represented 180° of the horizontal field, while across its transverse extent are spread only 40° - 50° of vertical field, thus implying a considerable distortion of the circles of equi-angular deviation of the field in the course of their projection on to the collicular surface. These circles of the field become distorted into ellipses on the collicular surface; the long axes of the ellipses lie in a transverse plane and represent the distorted projection of the vertical meridian, whereas the short axes lie antero-posteriorly to represent the horizontal meridian.

The meridians radiate out from the center, but are spaced apart unequally; those between 180° - 220° enclose between them the greater part of the surface of the anterior half of the colliculus, while the meridians between 0° - 30° take up the greater part of the surface of the posterior half. This disproportionate representation confines the meridians between 220° - 360° to a relatively narrow area on the lateral aspect of the colliculus, and the meridians between 30° - 180° to a narrow strip on the medial border.

These results, particularly those of Experiment R_3 Figure 33, Experiment R_7 Figure 34 and Experiment

R₁₉ Figure 37, demonstrate that the 200° - 220° meridians undergo even further distortion in the peripheral field, corresponding to an angular deviation of 50° - 75° . In the antero-lateral part of the colliculus, where this area of the field is represented, the meridians are seen to diverge from each other, enclosing between them a proportionately larger area of collicular surface. The areas devoted to the representation of 10° sectors in this part of the field is seen to be made yet greater by the wider spacing apart of 50° - 60° - 70° arcs. In a similar manner, though to a less marked extent, Figure 33 and Figure 37 show an increase in the areas of collicular surface devoted to the representation of the sectors of the peripheral field lying between the meridian of 0° - 30° and the arcs of angular deviation of 40° - 60° .

(ii) Magnification Factor Studies.

The distortion of the circles of equi-angular deviation of the field (i.e. parallels) into ellipses on the collicular surface implies a continuous gradation of values of the magnification factor between points situated along the major and minor axes of the ellipse, these values being maximal for points along the major axis (i.e. vertical

meridian) and minimal for those along the minor axis (i.e. horizontal meridian).

Figures 38 and 39 illustrate the variations of magnification factor with retinal eccentricity obtained from 5 experiments.

The magnification factors along the vertical axis are maximal at the center (mean 0.137 mm./degree, range .110 to .162) falling off rapidly to a mean value of 0.030 mm./degree, range 0.014 to .043 at 35° above and below fixation point.

The magnification factors along the horizontal meridian show remarkably little alteration with retinal eccentricity, with but a suggestion that the values are higher at the center and at a distance of 55° away from it than between them, both in the anterior and posterior fields, vide Table I. (page 124).

These magnification factor curves demonstrate quantitatively the differential distortion of the field about its horizontal and vertical axes, yet being an index expressing only linear distortion is inadequate to demonstrate the relatively large areas of collicular surface devoted to the representation of the field sectors at the anterior and posterior ends of the rabbit's band of vision, for the divergence of the meridians, one from the other,

TABLE I

POSTERIOR FIELD

ANTERIOR FIELD

	55°	35°	5°	5°	35°	55°
Retinal Eccentricity						
Range of Magnification Factors (M)	.025--.052	.025--.040	.025--.061	.025--.075	.025--.038	.025--.050
Mean Value of M	.039	.032	.040	.047	.030	.038
Standard Error Mean	± .005	± .002	± .006	± .004	± .001	± .004

in this region is a conspicuous feature of the collicular projection.

(iii) Retinal Ganglion Cell Concentrations.

Ganglion cell counts were made from horizontal sections of the retina 10 microns thick. A series of 15 slides containing the optic nerve head, the myelinated nerve fiber band, and the area of retina immediately below it were chosen; each section was separated from the next of the series by a distance of 400 microns, and consequently the ganglion cell counts were representative of a horizontal strip of retina 6 mm. wide. Each section was divided into segments of 300 microns, and the ganglion cells in each of these segments counted, noting also the presence of the optic nerve head and myelinated band. These results enabled a reconstruction of the horizontal strip of retina to be made, on which the positions of the disc and nerve fiber band could be denoted, while "contour" lines joining areas of retina with equal ganglion cell counts demarcated the ganglion cell concentrations - Figure 40.

These contour lines mark out a narrow band of retina lying parallel to, and slightly below, the myelinated band wherein the cell concentration

is uniformly high throughout its length; at each end this narrow band flares out to form a slightly widened area, the enlargement in the temporal retina being slightly more prominent than that in the nasal.

This pattern of retinal ganglion cell distribution relates well with the variations of magnification factor with retinal eccentricity along the horizontal and vertical axes of the visual field. This confirms the evidence obtained from projection studies, that the visual field of the rabbit is a narrow horizontal band with fairly uniform representation along its length, the representation across the width of the band being much higher at the center and falling off sharply along the narrow extent to which it is represented.

The position of the myelinated nerve fiber band was determined in three experiments, by determining its projection on the perimeter with the use of an Indirect Ophthalmoscope. Figures 34, 35, and 36 reveal that the myelinated nerve fiber band lies parallel to the band shaped visual field and so lies tilted to the same extent as the visual field.

The field of vision of the anaesthetized rabbit, fitted in the stereo-taxic head holder, is hence a

narrow band rotated by about 30° around its optic axis, such that the nasal field is directed downwards, while the temporal end of the band is directed upwards. In an effort to determine the position of the band of vision in the intact and unrestrained rabbit, the position of the myelinated band was observed by direct ophthalmoscopy in six rabbits. In these animals, the eye is so held that the myelinated band is truly horizontal, giving the normal rabbit a horizontal band shaped field of vision.

In 5 experiments the response of the deeper layers of the colliculus were recorded, the results of two of them being reproduced - Experiment R₂₃ Figure 41, and Experiment R₂₄ Figure 42. With the electrode tip on the collicular surface, the receptive fields obtained have been small, 2° - 5° , circular or very slightly oval in shape - the responses from the center of the band, and from its ends being larger in amplitude and more sharply localized than those obtained from the intervening areas. In the depths of the colliculus receptive fields become oval or ellipsoid, becoming progressively larger in size with increasing depth of the electrode. In the results illustrated, the surface positions of the electrode on the colliculus are denoted, and in the visual field the successive

changes in size and position of the receptive field as the electrode is advanced in 500 micron steps. The size of each field is indicated by points which lie at the center and at the terminal ends of the major axis of the elliptical fields.

These results indicate that the receptive fields of units situated in the deeper layers of the colliculus are elliptical, each being so orientated that it has its long axis parallel to the band shaped field of vision and to the myelinated nerve fiber band. In addition, the fields become progressively larger in size in the deeper layers - at depths beyond 2.5 mms. from the surface some units have been sampled which have receptive fields corresponding to the size, shape and disposition of the entire visual field.

Fig. 1

The position of the cat in the stereotaxic head holder, with eye-rings, jaw clamp and electrode-bridge assembly in situ.

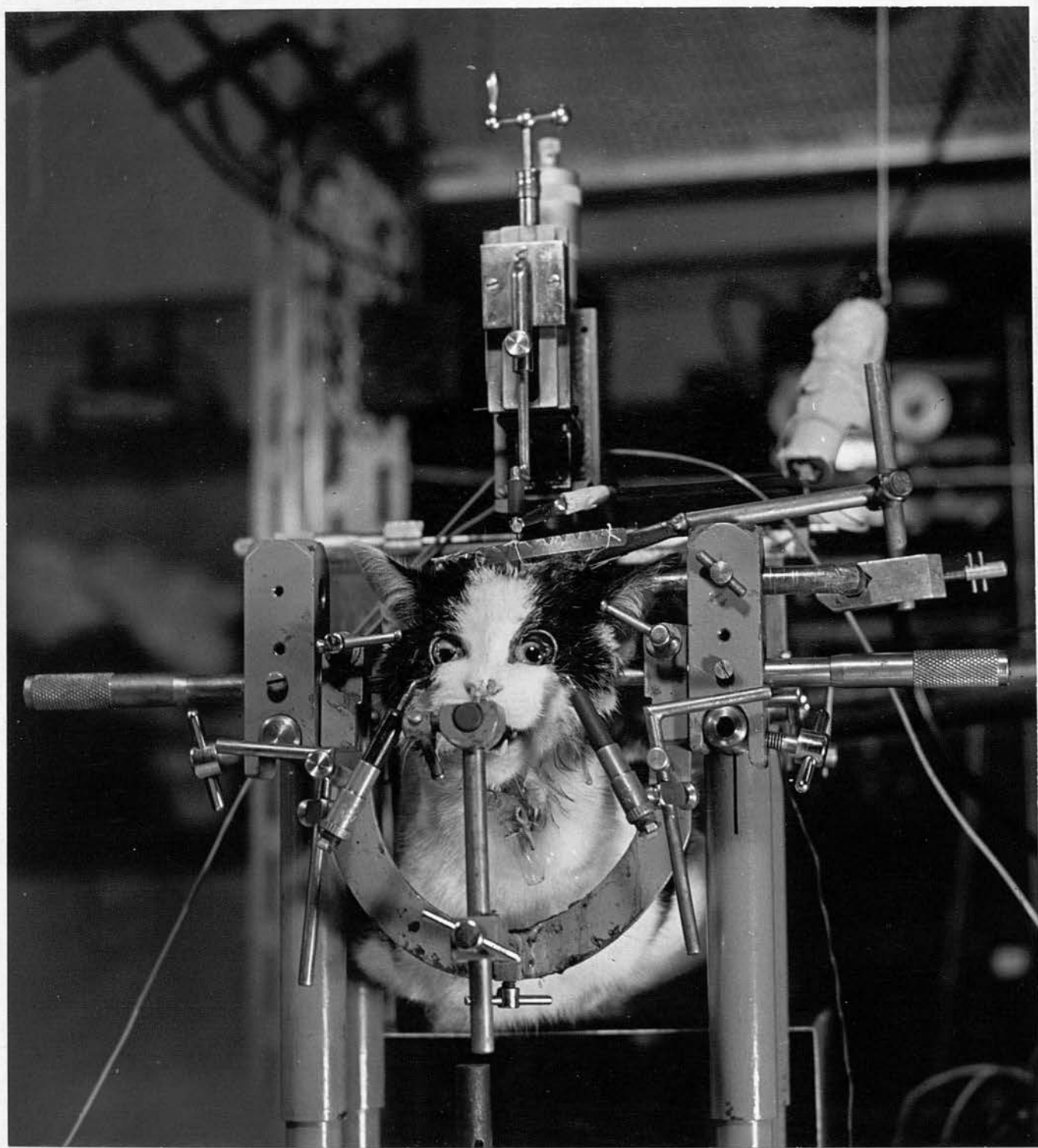


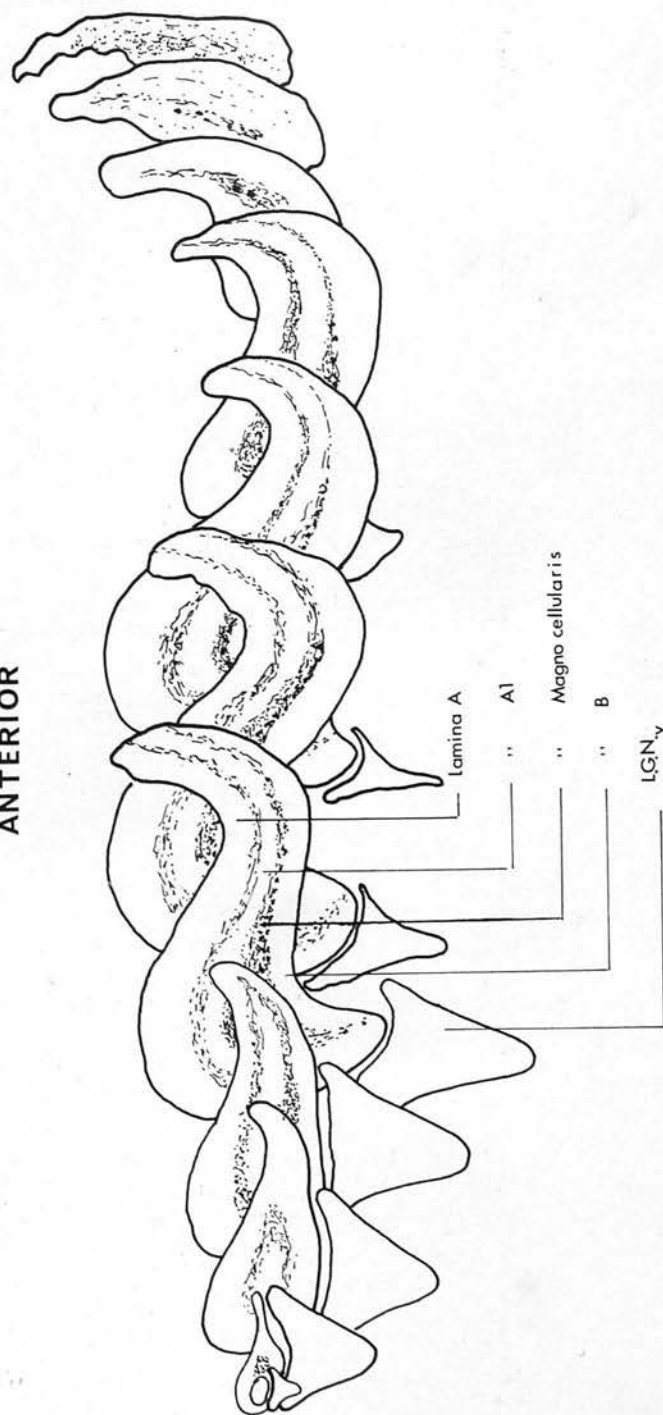
Fig. 2

Reconstruction of the left L.G.N. from serial parasagittal sections, to display the shape of the dorsal and ventral nuclei and disposition of the laminae.

100 μ Toluidine blue section; every sixth section has been represented.

ANTERIOR

MEDIAL



SERIAL PARA-SAGITTAL SECTIONS OF LEFT LATERAL GENICULATE NUCLEUS.

Fig. 3

Parasagittal section through right cerebral hemisphere, to show course of 7 electrode tracks, and relation of the L.G.N. to other cerebral structures.

100 μ Toluidine blue stained section, right border of picture directed anteriorly, linear magnification x 4.

Fig. 4

Parasagittal section through right L.G.N. to show course of 3 electrode tracks through the nucleus, and details of lamination. The lamina magnocellularis forms here, a well defined layer of cells in the thickened anterior region of the nucleus, and the Nucleus Perigeniculatus Anterior, an ill defined stratum of cells lying over the dorsal surface of the pars dorsalis.

100 μ Toluidine blue, linear magnification x 12.

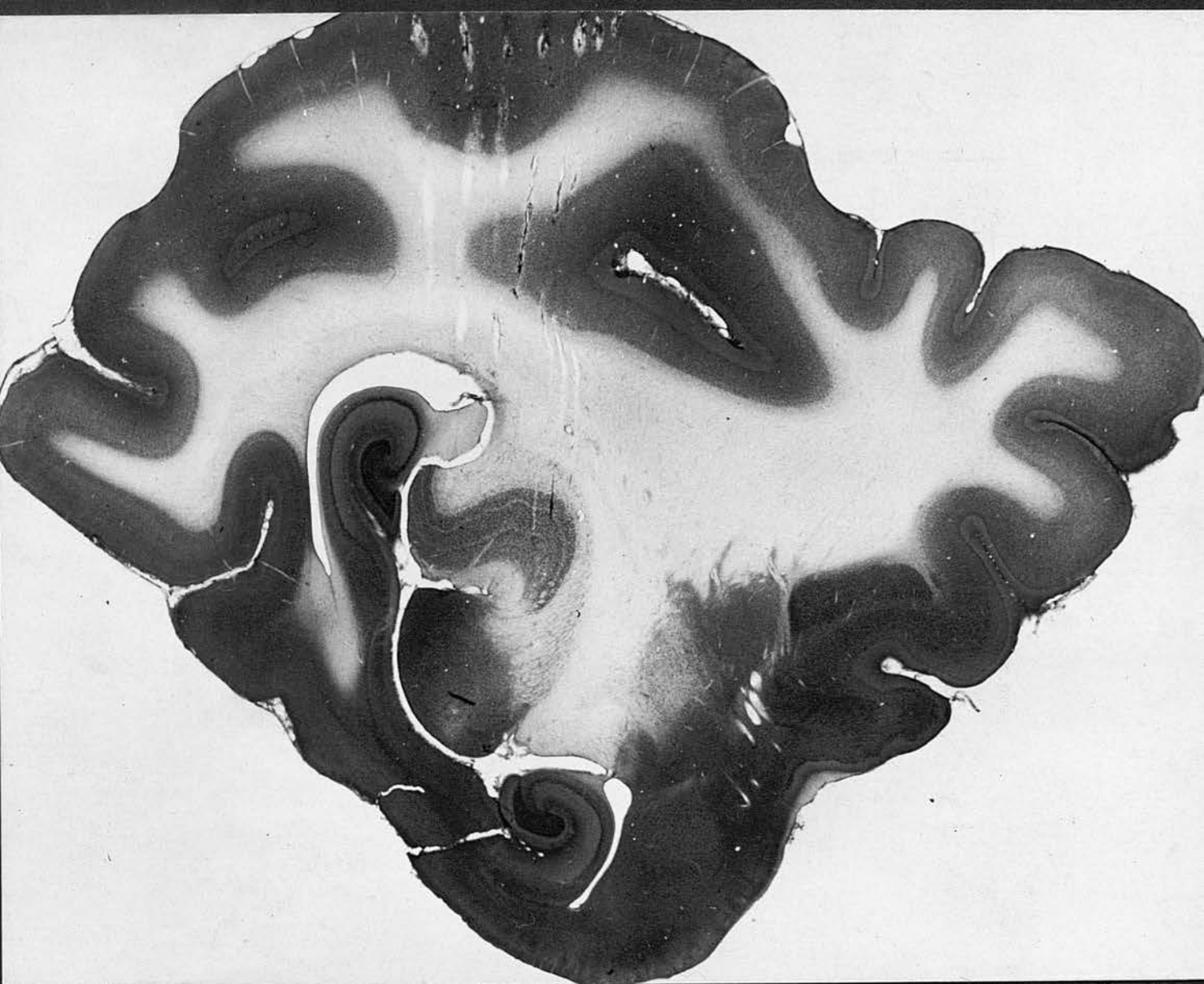


Fig. 5

Parasagittal section, left L.G.N., to show course of 3 electrode tracks. The posterior track traverses successively laminae B, A₁, A, A₁, B. This and all succeeding sections, 100 μ Toluidine blue, at linear magnification of 12.

Fig. 6

Parasagittal section, left L.G.N., to show course of 6 electrode tracks.

Fig. 7

Parasagittal section, left L.G.N. A single electrode track passes down the posterior vertical extent of the nucleus, along the length of lamina A.

Fig. 8

Parasagittal section, left L.G.N. Two electrode tracks in region of the Nucleus Interlaminaris Medialis.

Fig. 9

Transverse section, left L.G.N. Two electrode tracks through pars dorsalis; medially, the Nucleus Interlaminaris Medialis.

Fig. 10

Transverse section, right L.G.N. Infero-laterally the pars ventralis of the L.G.N. forms a small cap-shaped structure, medially, the characteristic appearance of the Nucleus Interlaminaris Medialis.

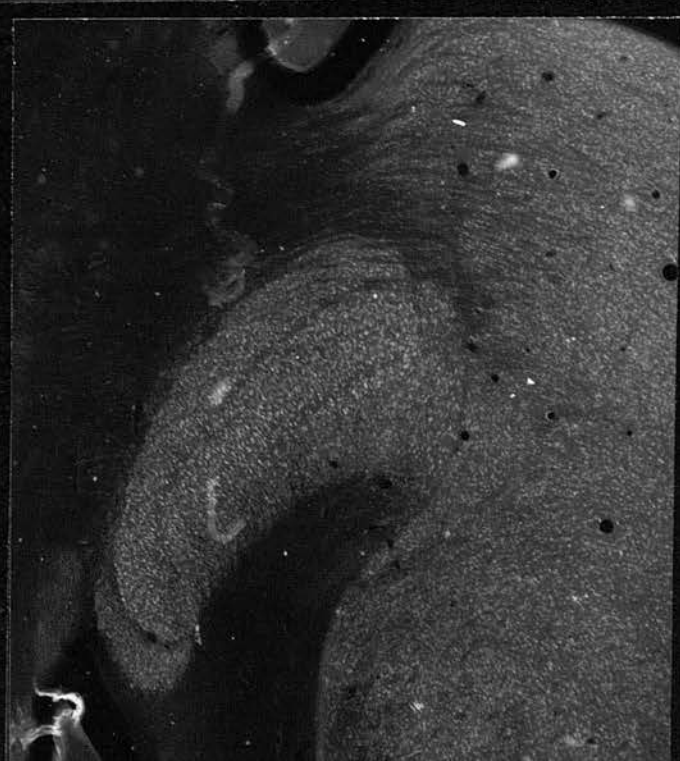
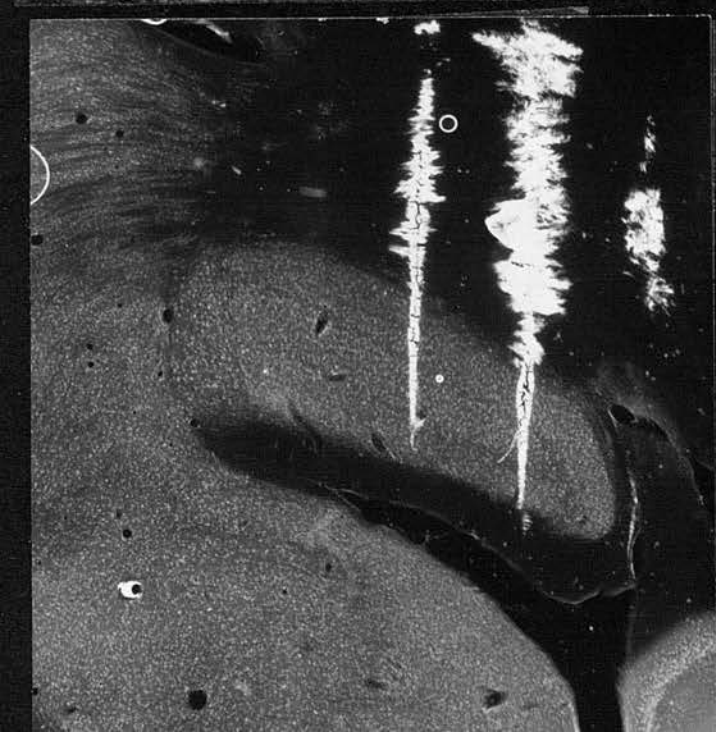
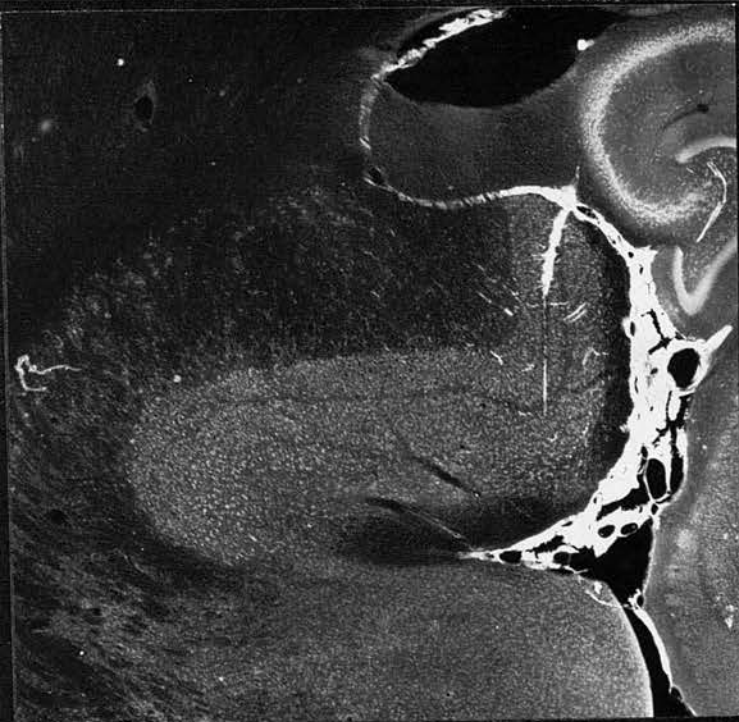
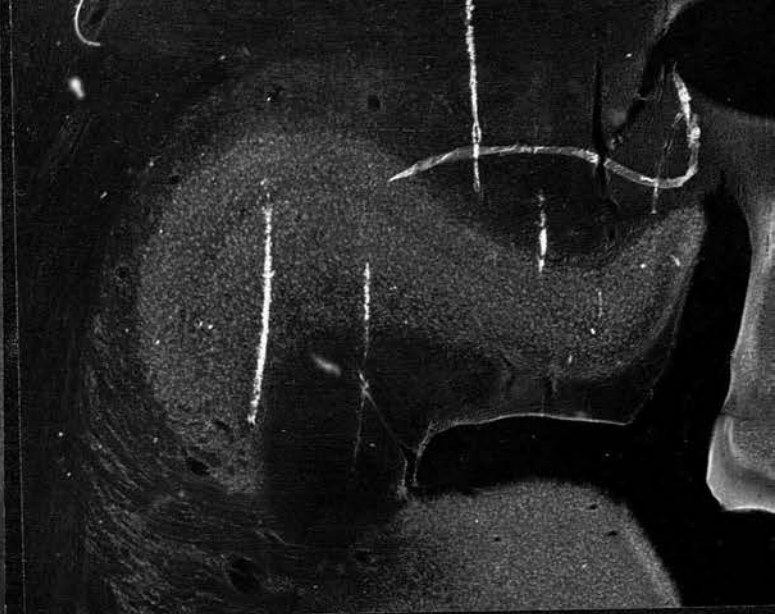
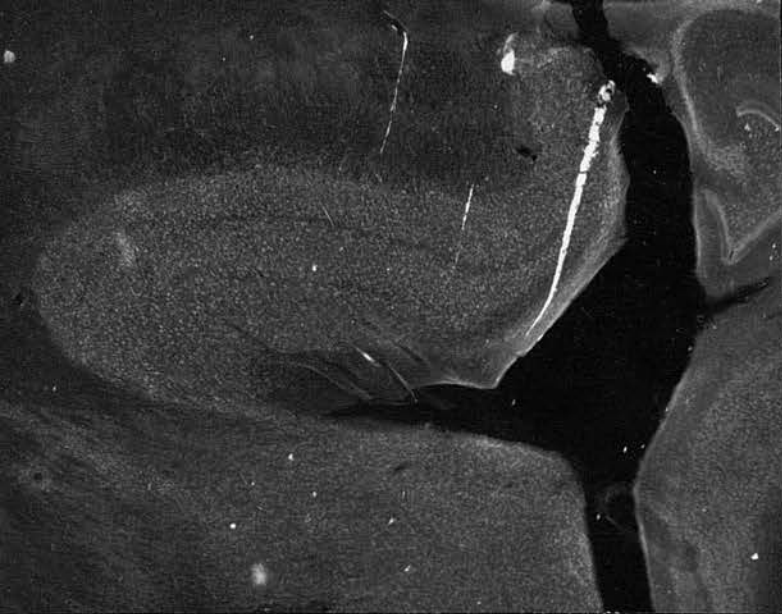
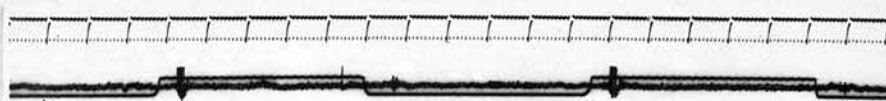
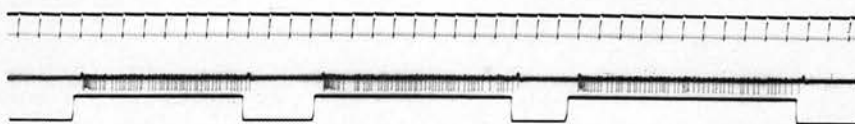


Fig. 11

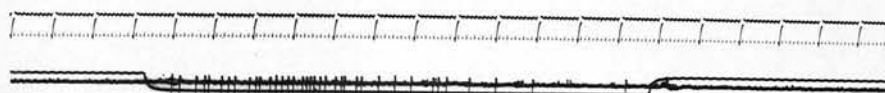
- A A short 'on' center response from upper aspect of lamina A.
In this and all succeeding records,
Time signal - 10 and 100 msec.
Stimulus signal moves up at 'on'.
- B Single unit response, showing continuous 'on' center activity.
- C Single unit response, continuous 'off' center activity, from deeper aspect of lamina A.
- D Perigeniculate cell response to a neon flash of short duration.
- E Multi-cellular 'on' center response from Visual II, i.e. Nucleus Interlaminaris Medialis.
- F Continuous 'off' center activity from cell in lamina B, showing complete inhibition at 'on'.
- G Continuous 'off' center activity in lamina B, showing incomplete inhibition at 'on'.
- H Single unit in lamina B showing short 'on', 'off' effects.
- I Single unit in lamina B showing continuous 'on' activity.



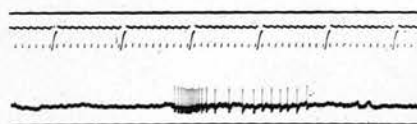
A



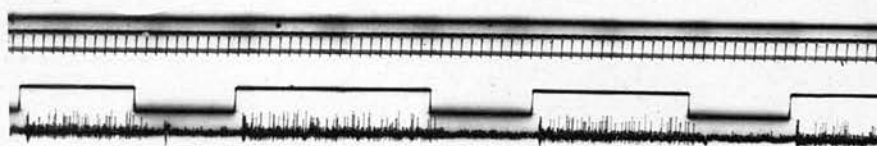
B



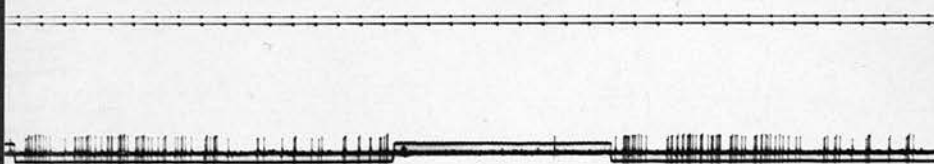
C



D



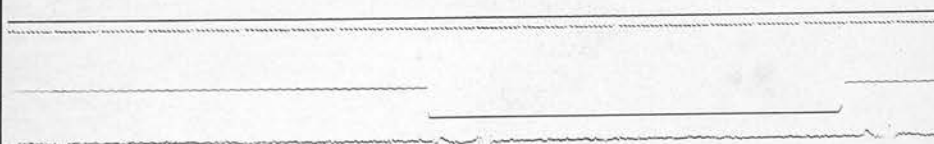
E



F



G



H

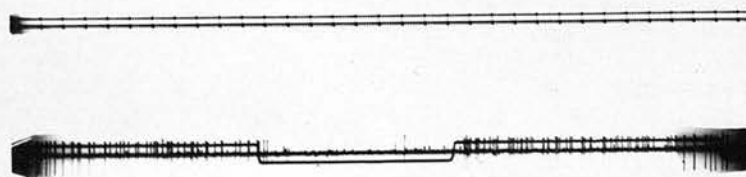
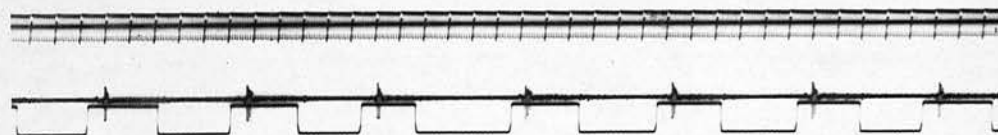
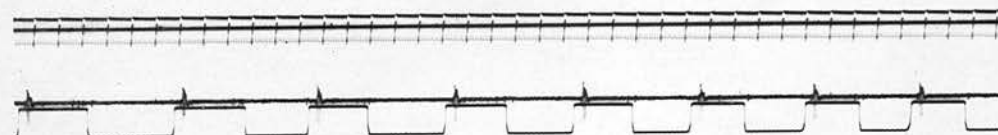


Fig. 12

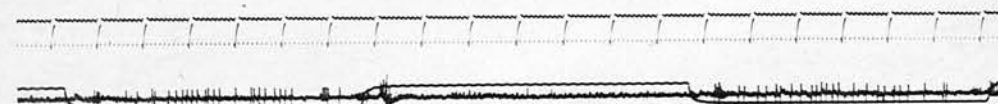
- J_1 Single unit showing short center 'on' response to a 1 mm. spot of light in the center of its receptive field.
- J_2 Same unit as in J_1 , response to a 10 mm. spot; summation producing a reduction in the latency of the response.
- K_1 Center 'off' effect with 1 mm. spot in center of receptive field.
- K_2 Same unit, with 5 mm. spot; peripheral inhibition reducing the size of the 'off' center discharge.
- L_1 Multi-unit 'off' center activity from lamina B - with no background illumination.
In L_1 , L_2 , L_3 stimulus signal moves up at 'off'.
- L_2 Same unit as in L_1 with some background illumination.
- L_3 Same unit, with further increase of intensity of background illumination.
Increasing intensity of illumination of peripheral field, causes increased inhibition of center 'off' effect.



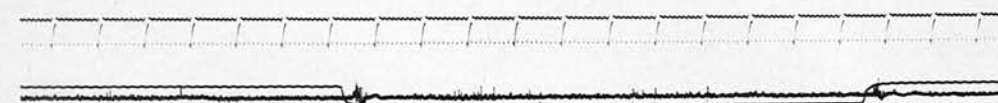
J₁



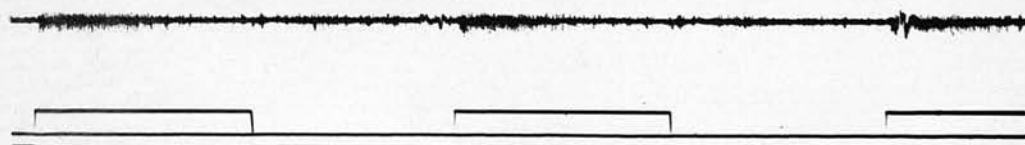
J₂



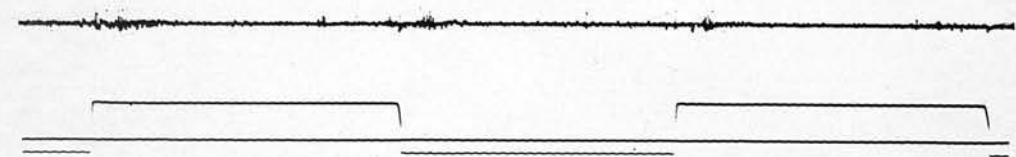
K₁



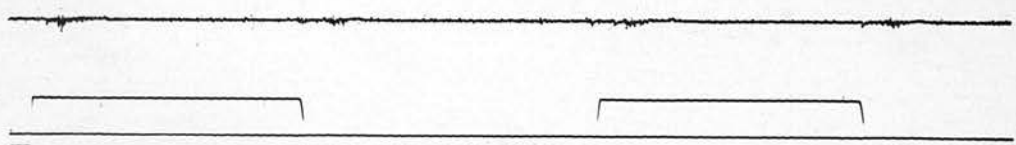
K₂



L₁



L₂

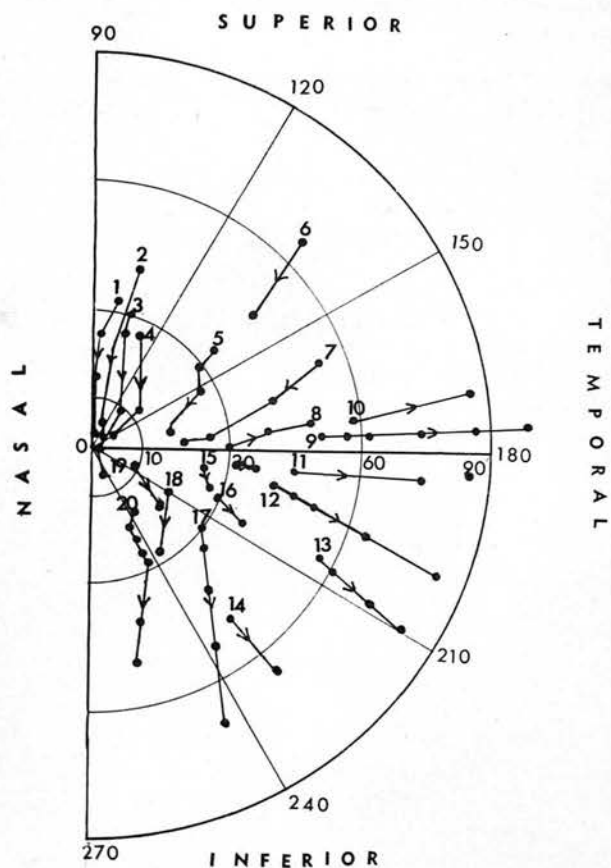


L₃

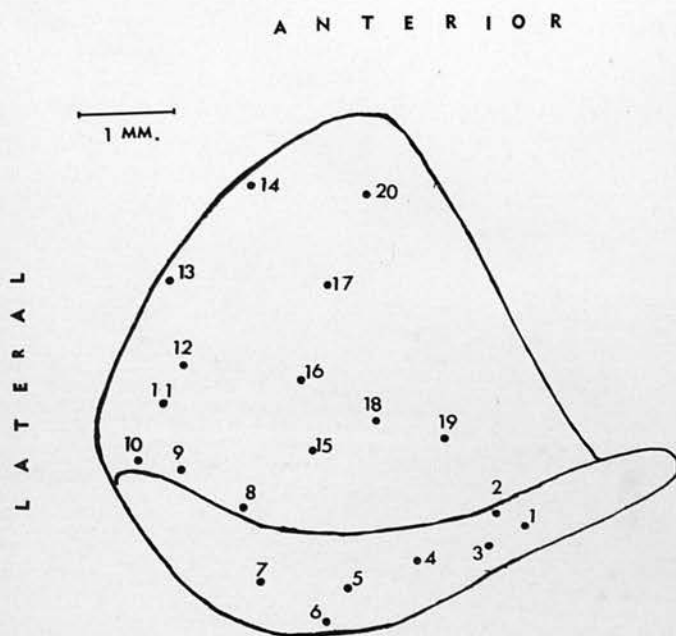
Fig. 13

Successive changes in position of localization in the visual field as electrode traverses thickness of lamina A, in different regions of the nucleus.

Composite diagram made from the results of 6 experiments.



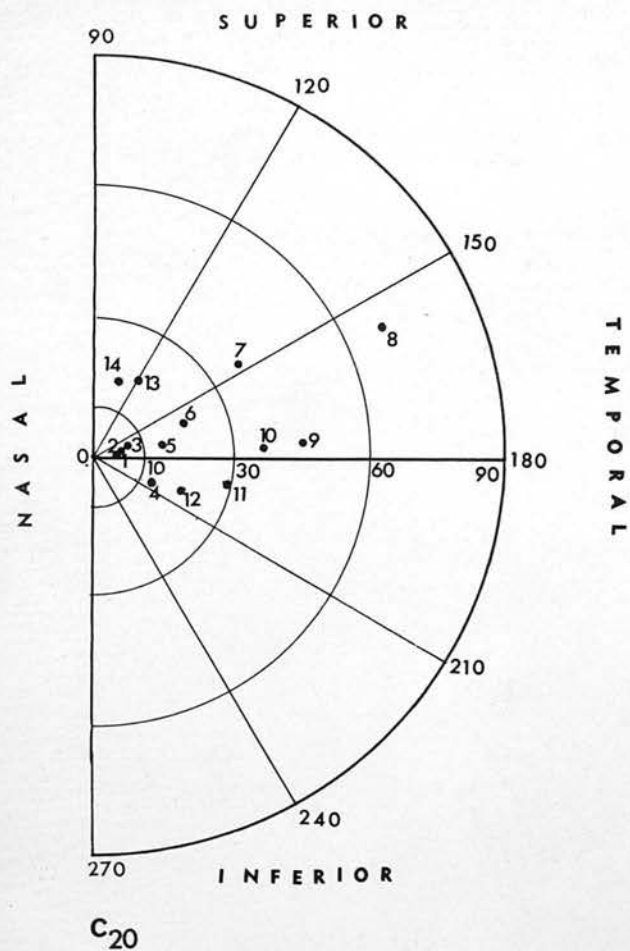
CAT. VISUAL HEMI-FIELD, RIGHT EYE.



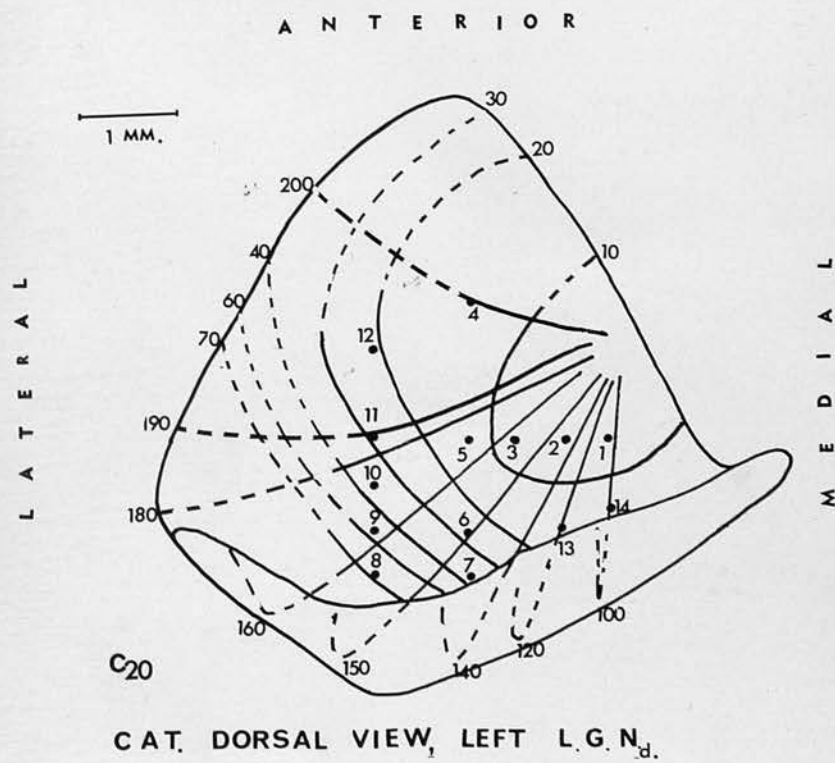
CAT. DORSAL VIEW, LEFT L.G.N._d.

Fig. 14

Experiment C₂₀. Projection of the visual hemi-field
of right eye on dorsal surface of lamina A of left L.G.N.



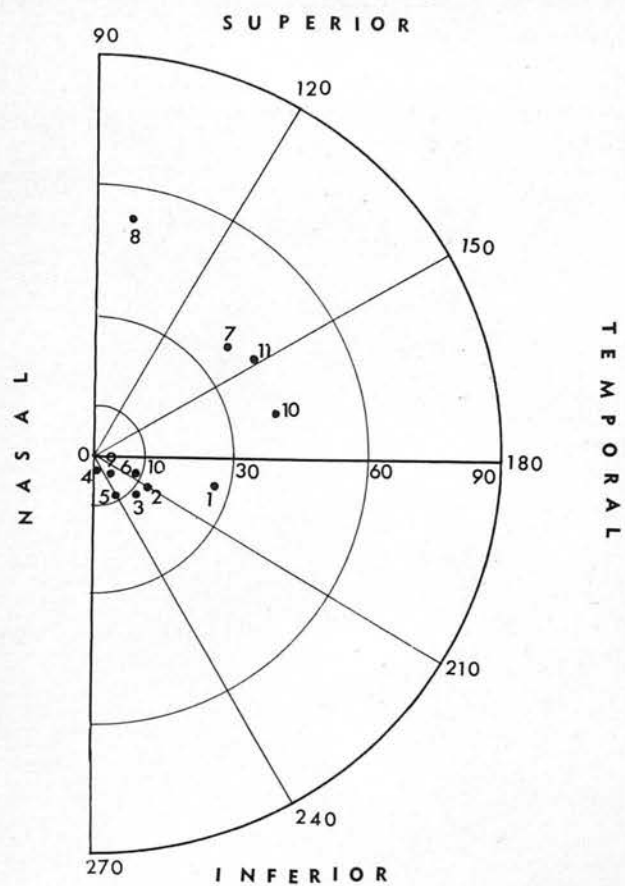
CAT. VISUAL HEMI-FIELD, RIGHT EYE.



CAT. DORSAL VIEW, LEFT L.G.N._d.

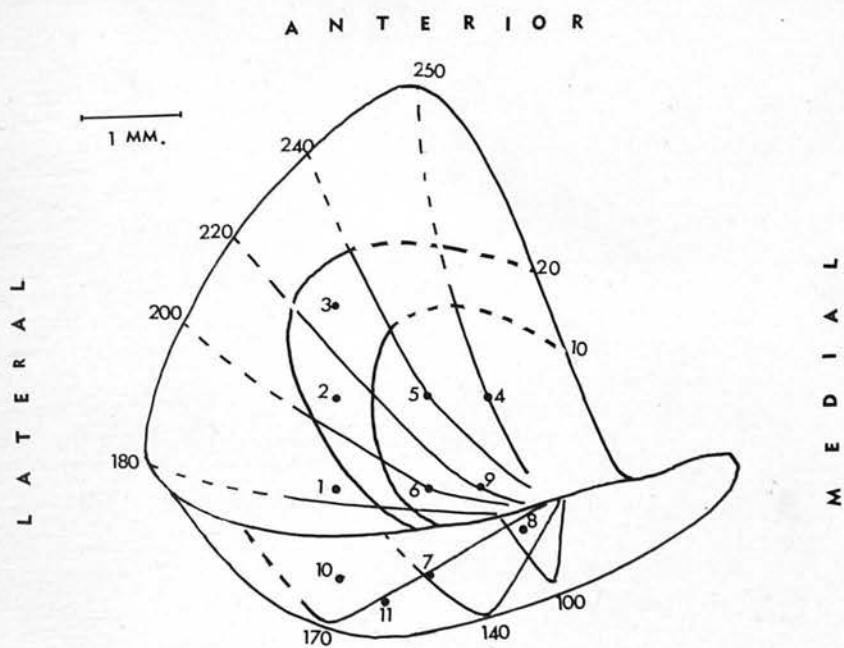
Fig. 15

Experiment C₂₃. Projection of the visual hemi-field
of right eye on dorsal surface of lamina A of the left L.G.N.



C₂₃

CAT. VISUAL HEMI-FIELD, RIGHT EYE.

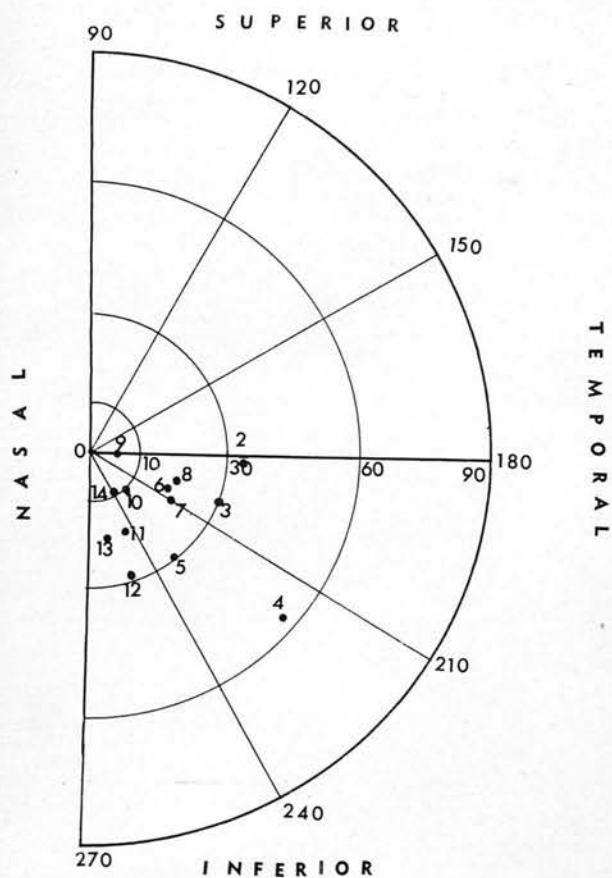


C₂₃

CAT. DORSAL VIEW, LEFT L.G.N._d.

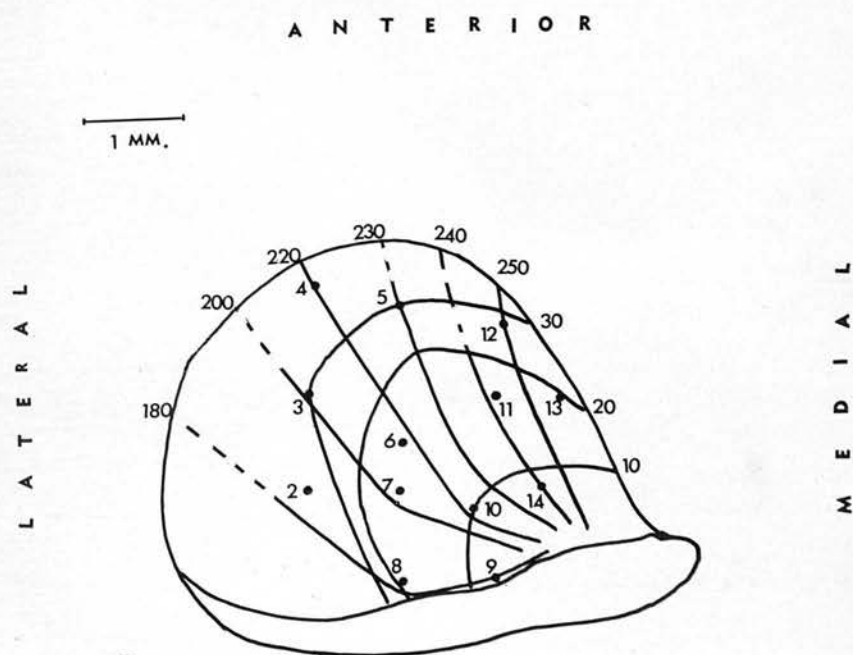
Fig. 16

Experiment C₂₈. Projection of the visual hemi-field
of right eye on the dorsal surface of lamina A of the left
L.G.N.



C28

CAT. VISUAL HEMI-FIELD, RIGHT EYE.



C28

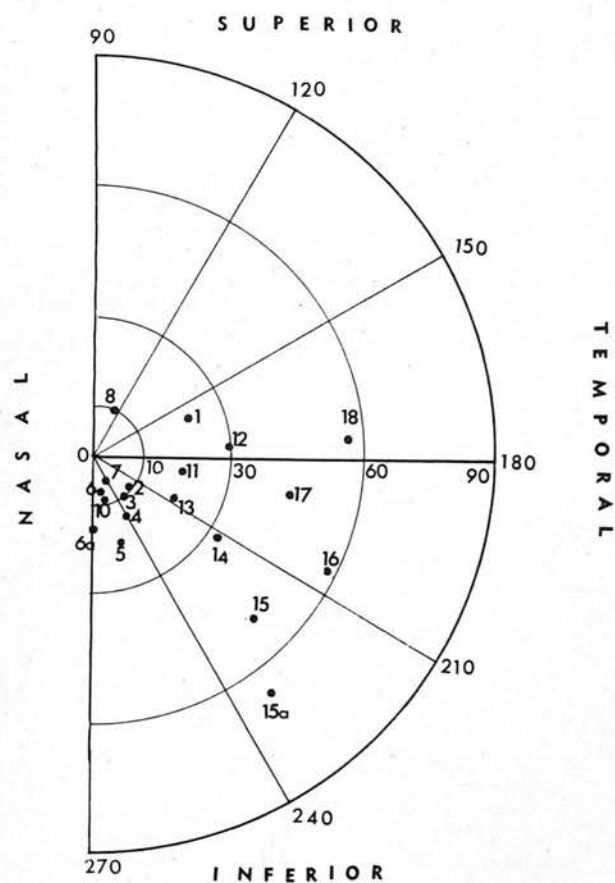
CAT. DORSAL VIEW, LEFT L.G.N._d.

Fig. 17

Experiment C₂₄. Projection of the visual hemi-field of the right eye on the dorsal surface of lamina A of the left L.G.N., and on the plane projection of the surface of the lamina.

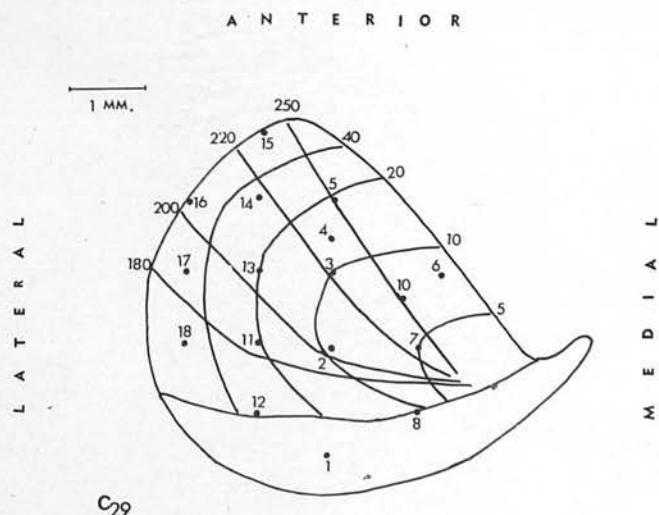
Fig. 18

Experiment C₂₉. Projection of the visual hemi-field of the right eye on the dorsal surface of lamina A of the left L.G.N. and on the plane projection of the surface of the lamina.



C₂₉

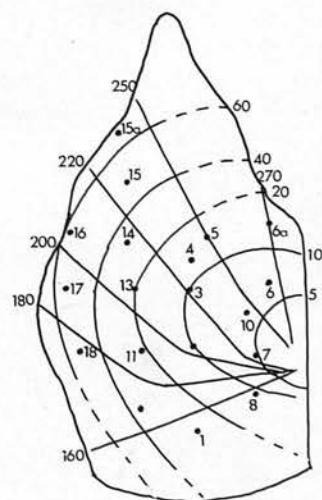
CAT. VISUAL HEMI-FIELD, RIGHT EYE.



C₂₉

CAT. DORSAL VIEW, LEFT L.G.N._d.

1 MM.

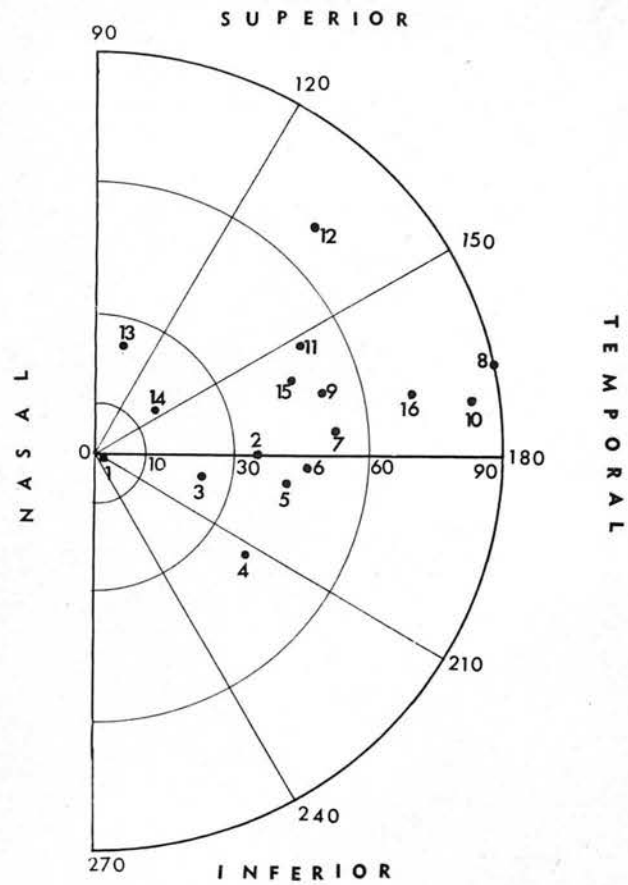


C₂₉

PLANE PROJECTION OF SURFACE OF LAMINA A

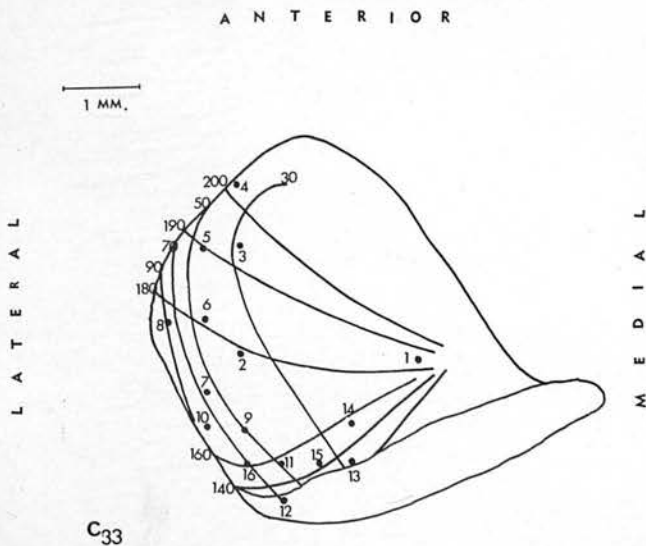
Fig. 20

Experiment C₃₃. Projection of the visual hemi-field of the right eye, on the dorsal surface of lamina A of the left L.G.N., and on the plane projection of the surface of the lamina.



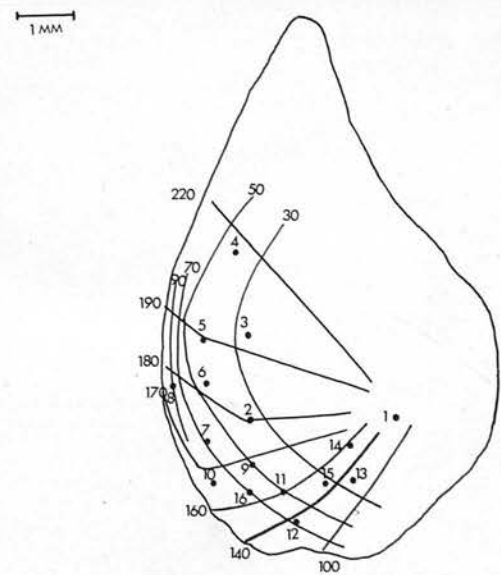
C₃₃

CAT. VISUAL HEMI-FIELD, RIGHT EYE.



C₃₃

CAT. DORSAL VIEW, LEFT L.G.N.d.



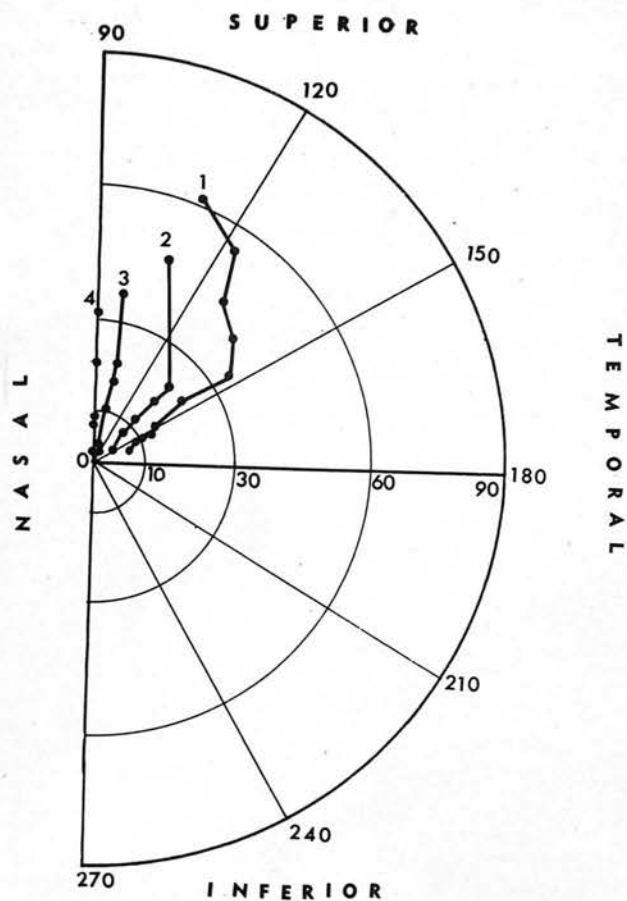
C₃₃

PLANE PROJECTION OF SURFACE OF LAMINA A

Fig. 21

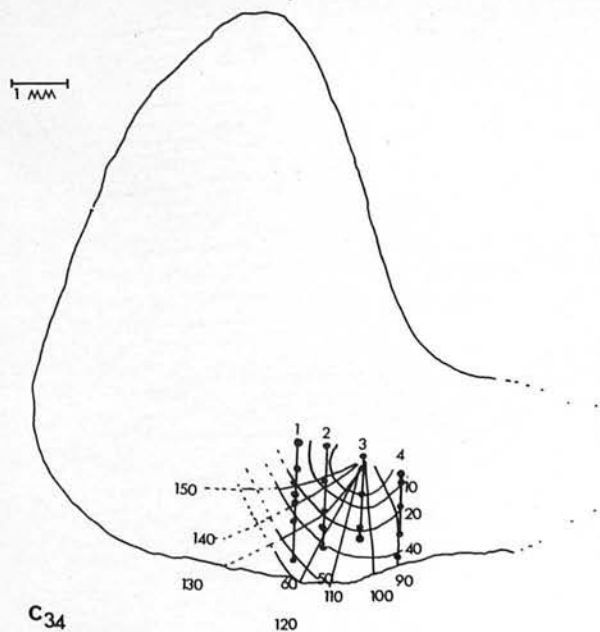
Experiment C₃₄. Projection of the visual hemi-field of the right eye on the surface of the posterior vertical curl and on the plane projection of its anterior surface.

In this experiment the electrodes travelled down along the length of the lamina A, the successive changes in localization in the visual field are denoted by continuous lines on the field chart.



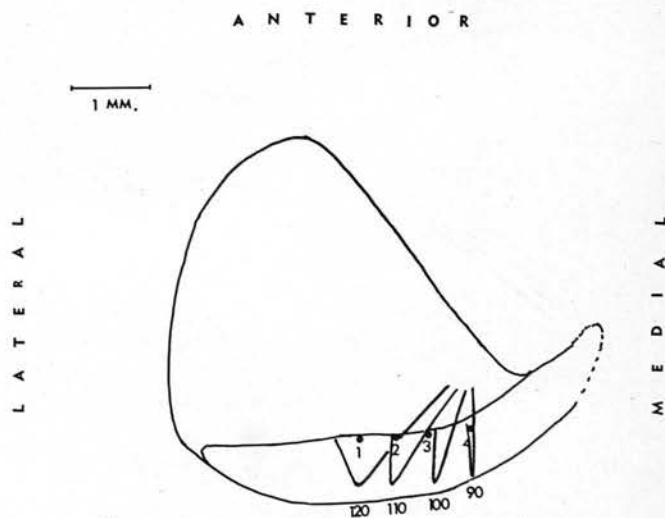
C₃₄

CAT. VISUAL HEMI-FIELD, RIGHT EYE.



C₃₄

PLANE PROJECTION OF SURFACE OF LAMINA A



C₃₄

CAT. DORSAL VIEW, LEFT L.G.N._d.

Fig. 22

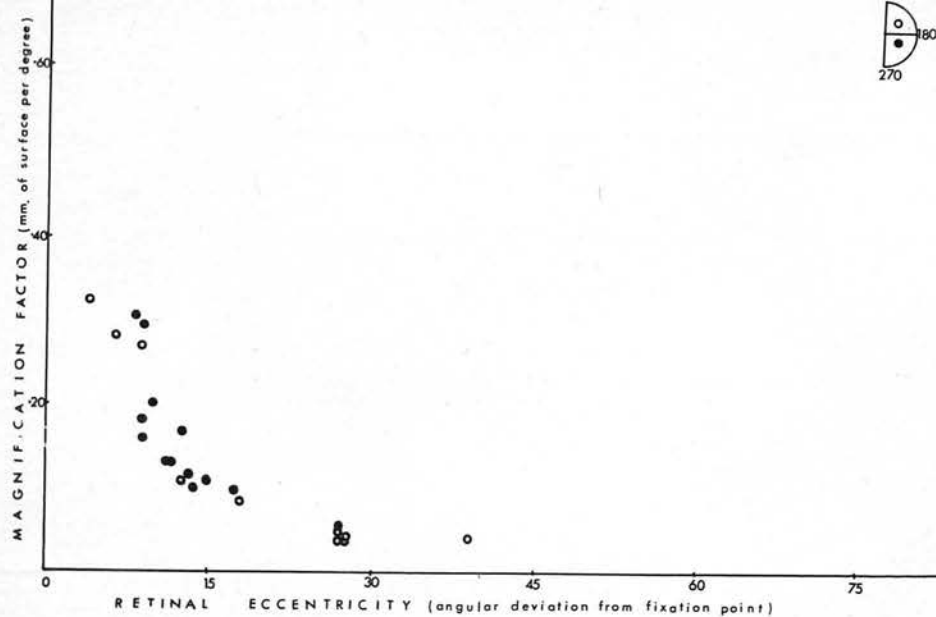
Experiment C_{15} . Variation of magnification factors
with retinal eccentricity.

Fig. 23

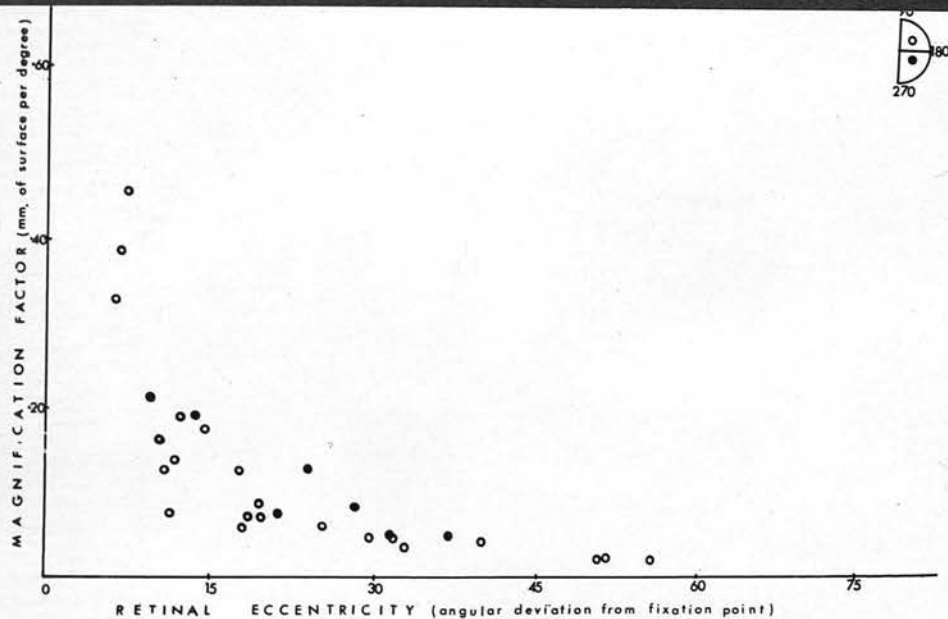
Experiment C_{20} . Variation of magnification factors
with retinal eccentricity.

Fig. 24

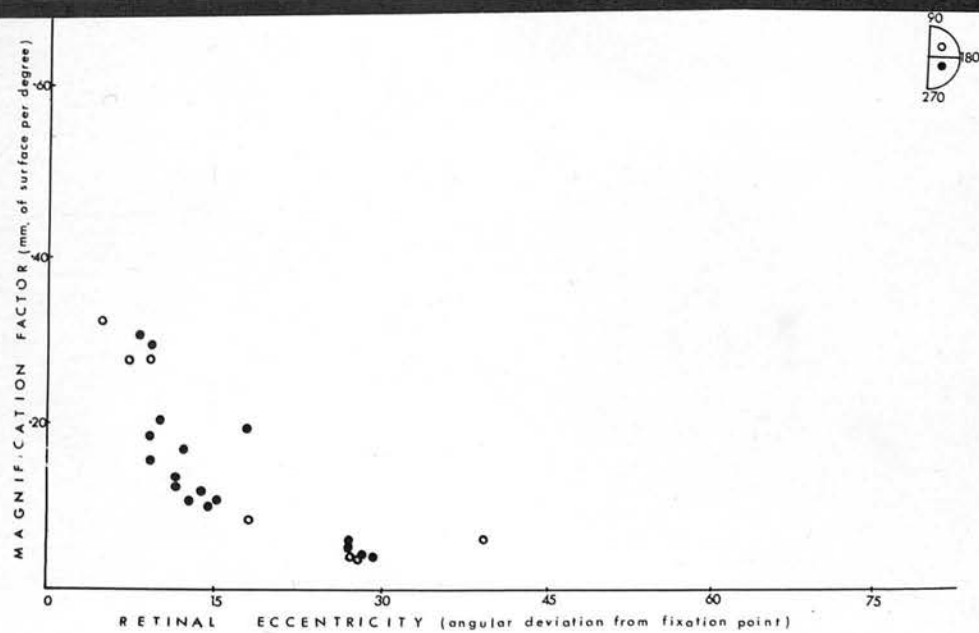
Experiment C_{21} . Variation of magnification factors
with retinal eccentricity.



C15



C20



C21

Fig. 25

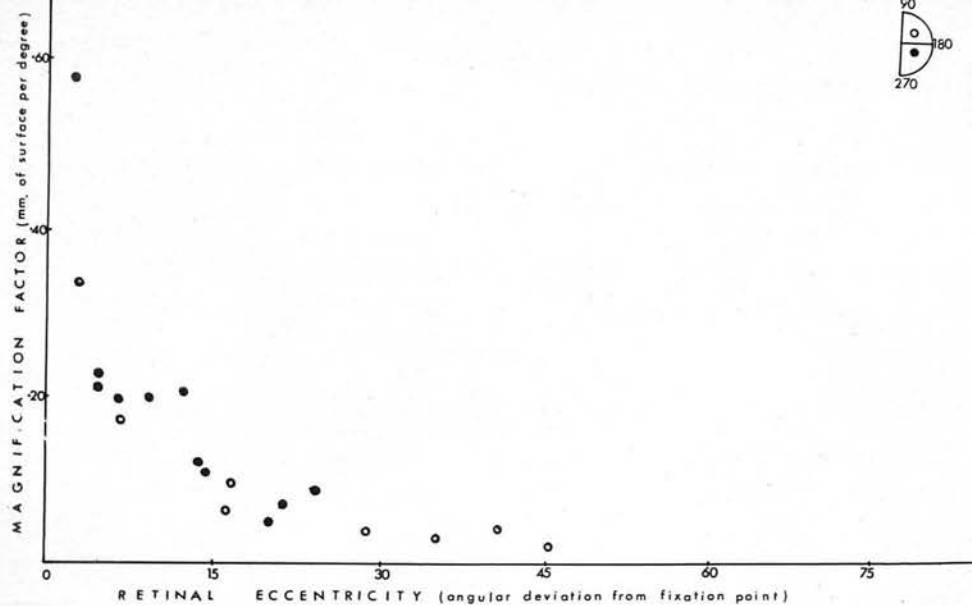
Experiment C₂₄. Variation of magnification factors
with retinal eccentricity.

Fig. 26

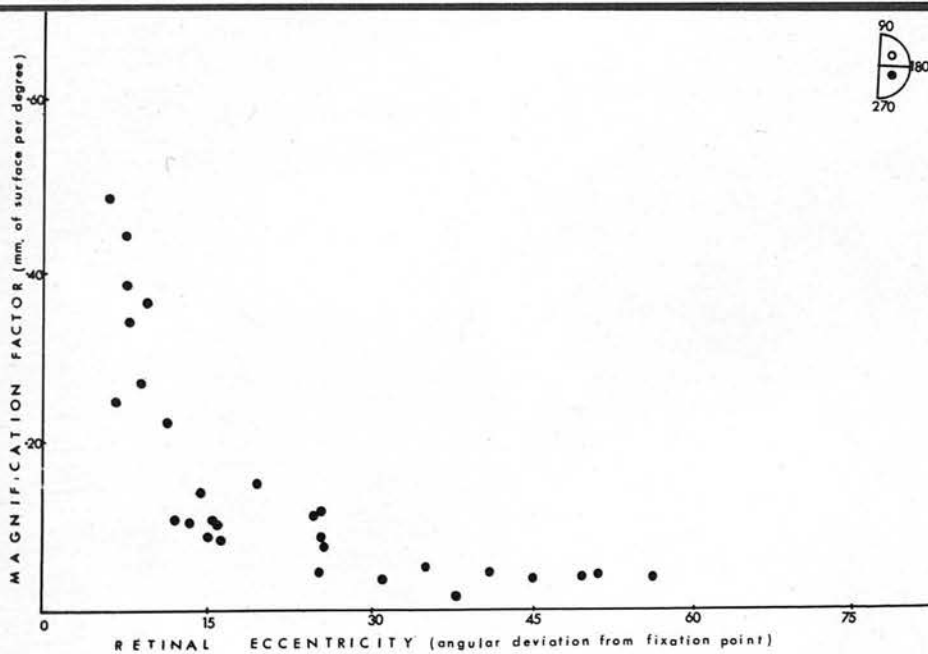
Experiment C₂₉. Variation of magnification factors
with retinal eccentricity.

Fig. 27

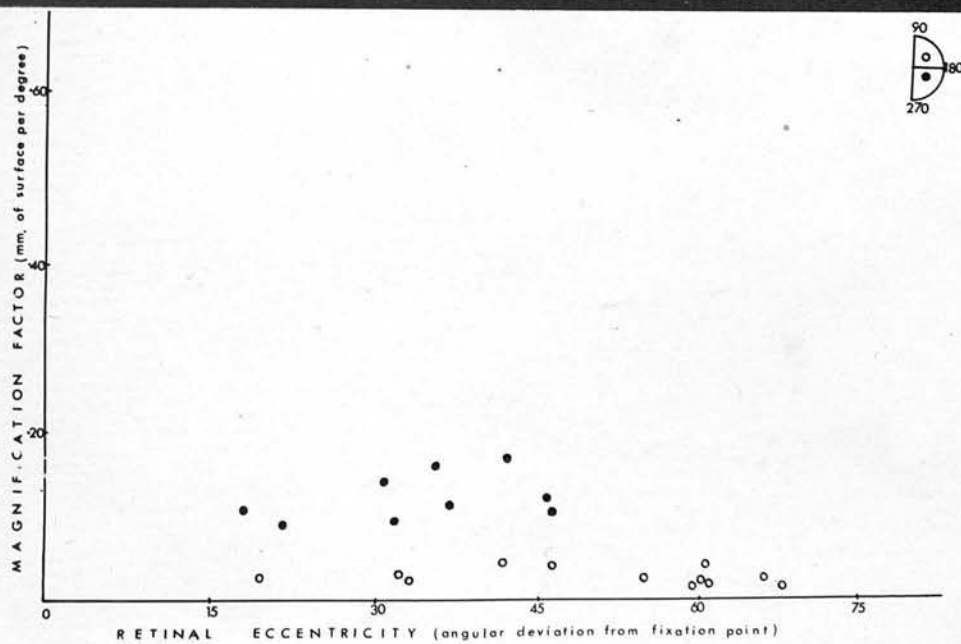
Experiment C₃₃. Variation of magnification factors
with retinal eccentricity.



C24



C29



C33

Fig. 28

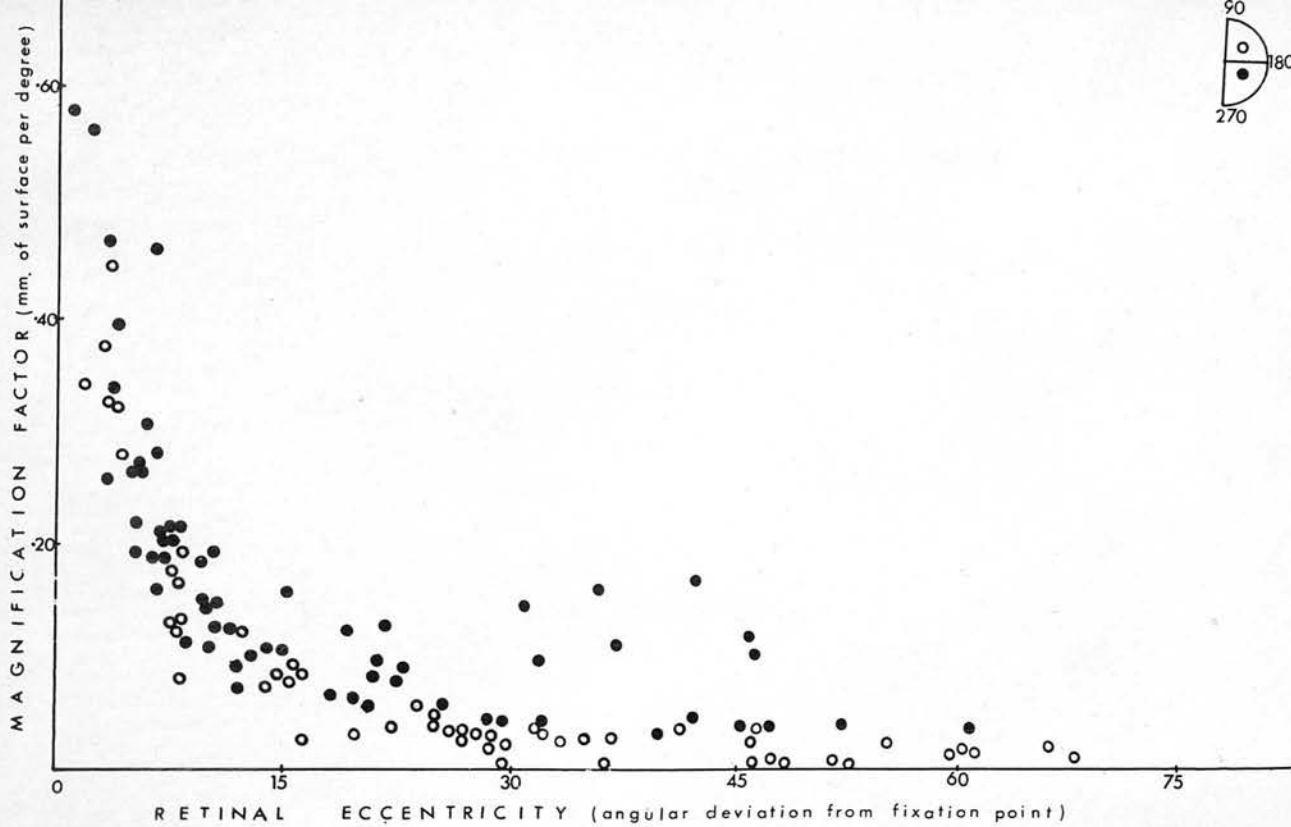
Composite results of Experiments C_{15,20,21,24,29,33} to show variation of magnification factors with retinal eccentricity, in upper and lower visual field quadrants.

Fig. 29

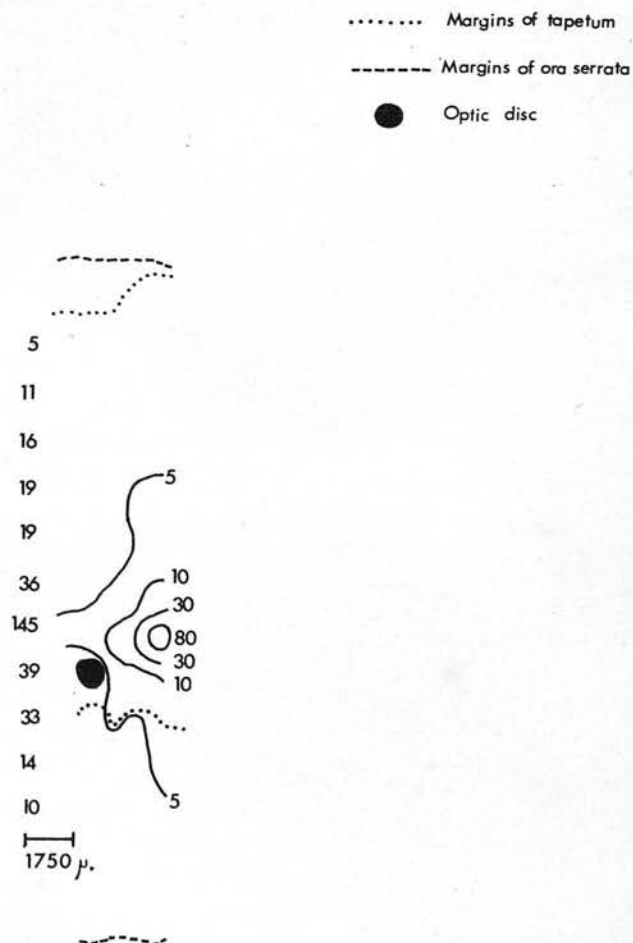
Retinal ganglion cell concentration 'contours'.

Vertical strip of retina containing optic disc and area centralis retinae, of left eye, as viewed from in front.

The column of figures on the left indicate the total number of ganglion cells in $\frac{1}{2}$ strips of retina 745μ wide at each horizontal level.



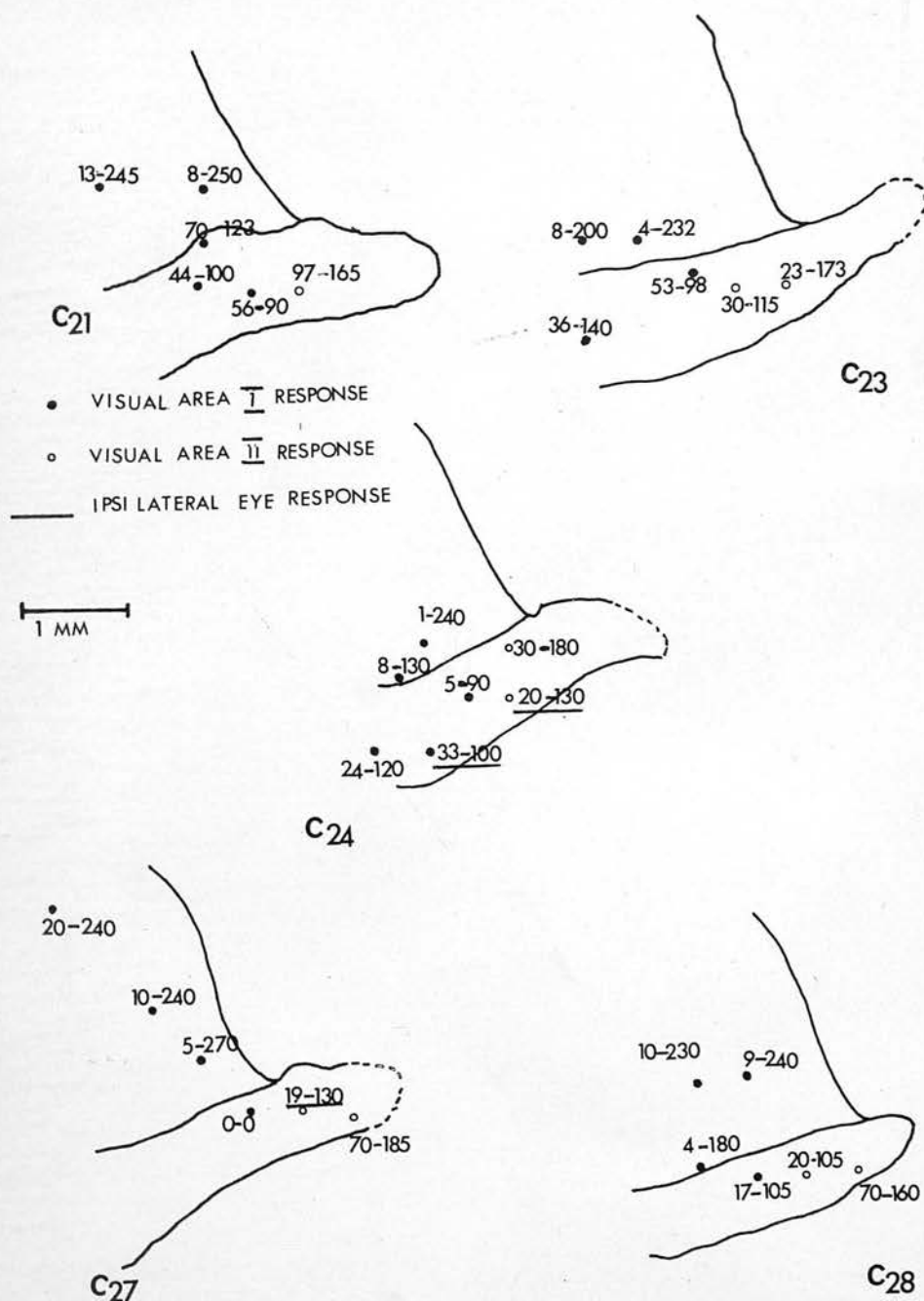
C₁₅; 20, 21, 24, 29, 33.



RETINAL GANGLION CELL CONCENTRATIONS.

Fig. 30

Composite diagram from results of Experiments C_{21,23,}
27,28, in which region of Nucleus Interlaminaris Medialis
was explored, for responses from Visual II.



DORSAL VIEW OF POSTERO-MEDIAL REGION
 OF LEFT L.G.N._d IN FIVE EXPERIMENTS.

Fig. 31

Rabbit in stereotaxic head-holder with jaw-clamp, eye-ring
and electrode-bridge assembly, in situ.

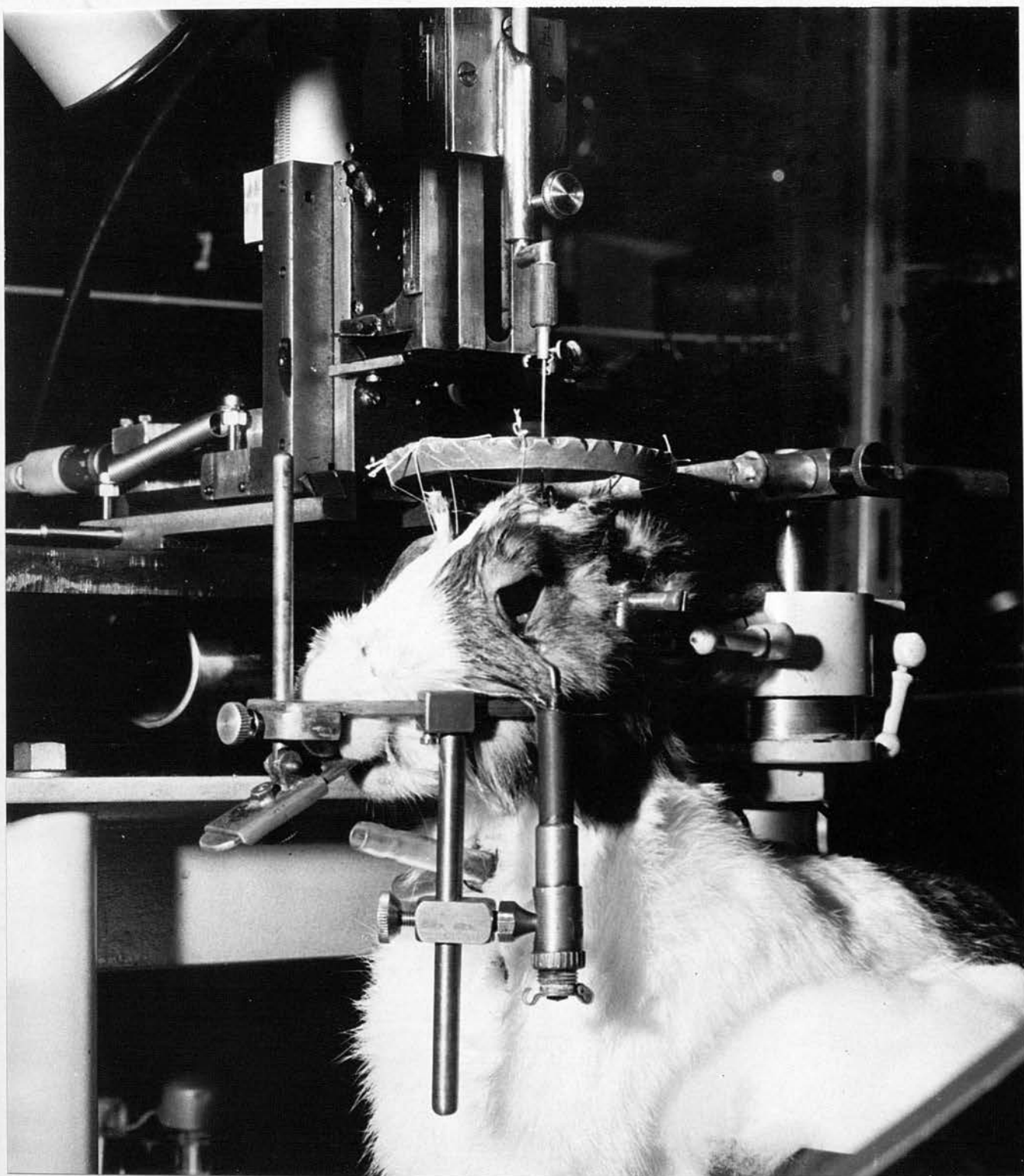


Fig. 32

- A. Multi-unit 'on' responses from collicular surface.
Time signal 10 msec.
Stimulus signal moves down at 'on'.
- B₁. Localized polyphasic responses from conducting medium
between inferior surface of cortex and dorsal surface
of colliculus.
- B₂. Localized colliculus surface response to short duration
neon flashes.
- C₁. Collicular "alpha" rhythm.
- C₂. Abolition of collicular "alpha" rhythm by intra-muscular
injection of 0.1 cc. Nembutal.

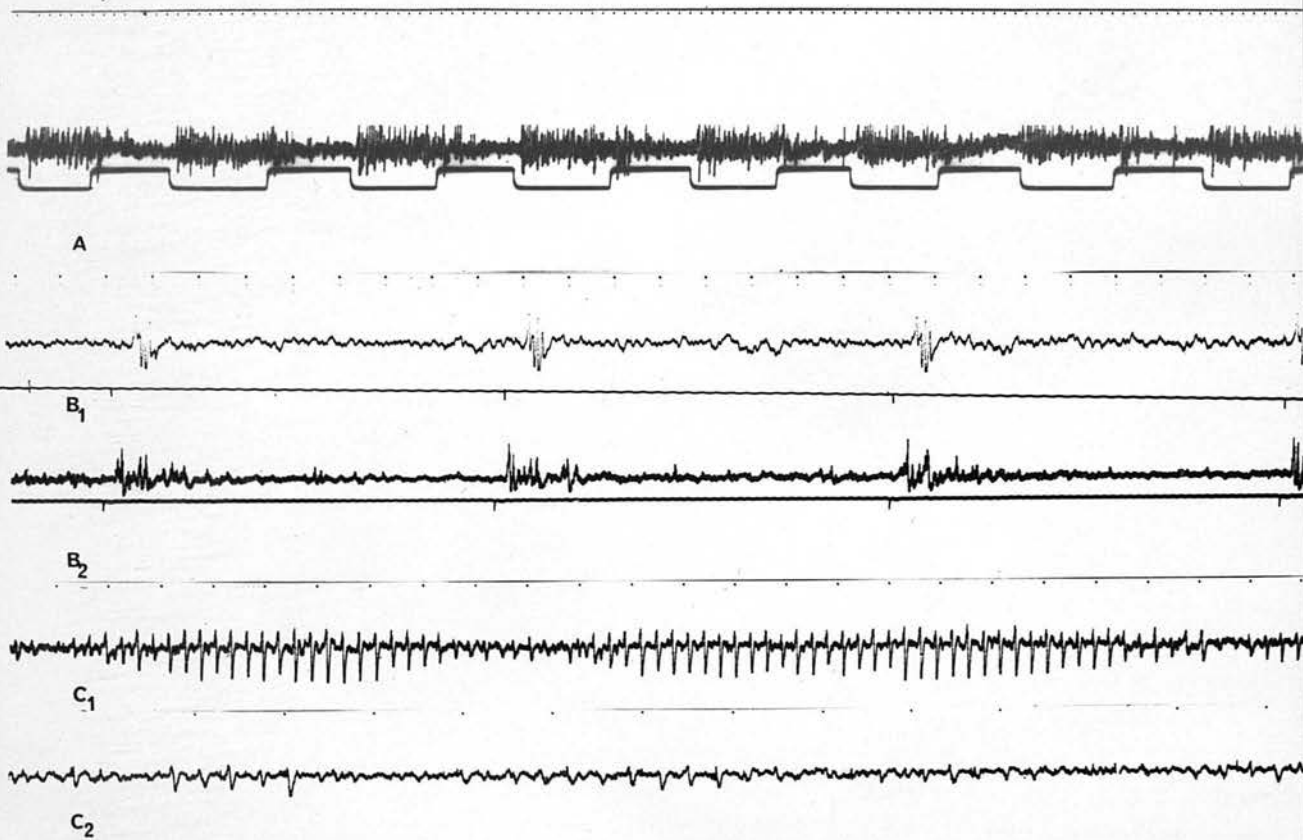
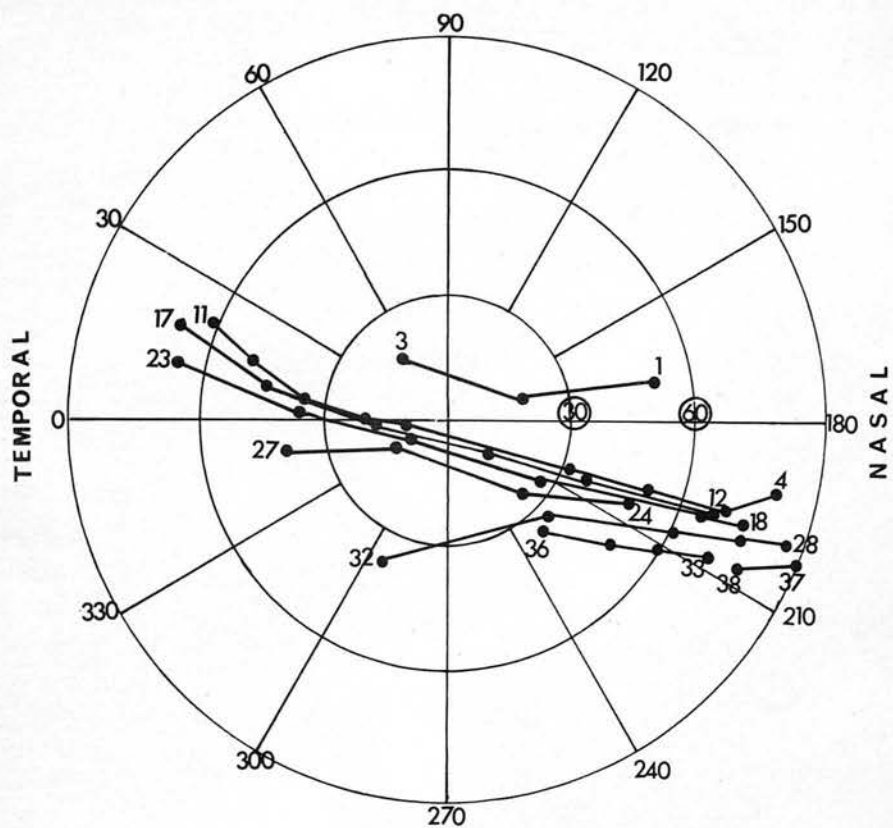


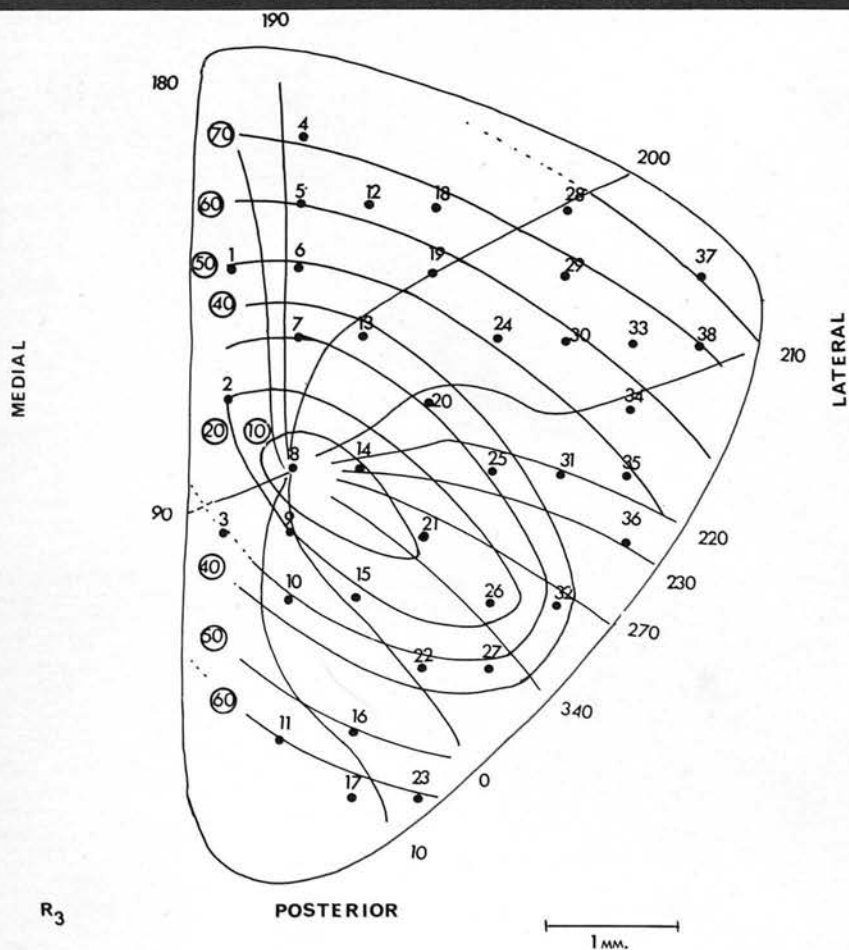
Fig. 33

Experiment R₃. Projection of visual field of left
eye on dorsal surface of right colliculus.



R_3

RABBIT, VISUAL FIELD OF LEFT EYE.



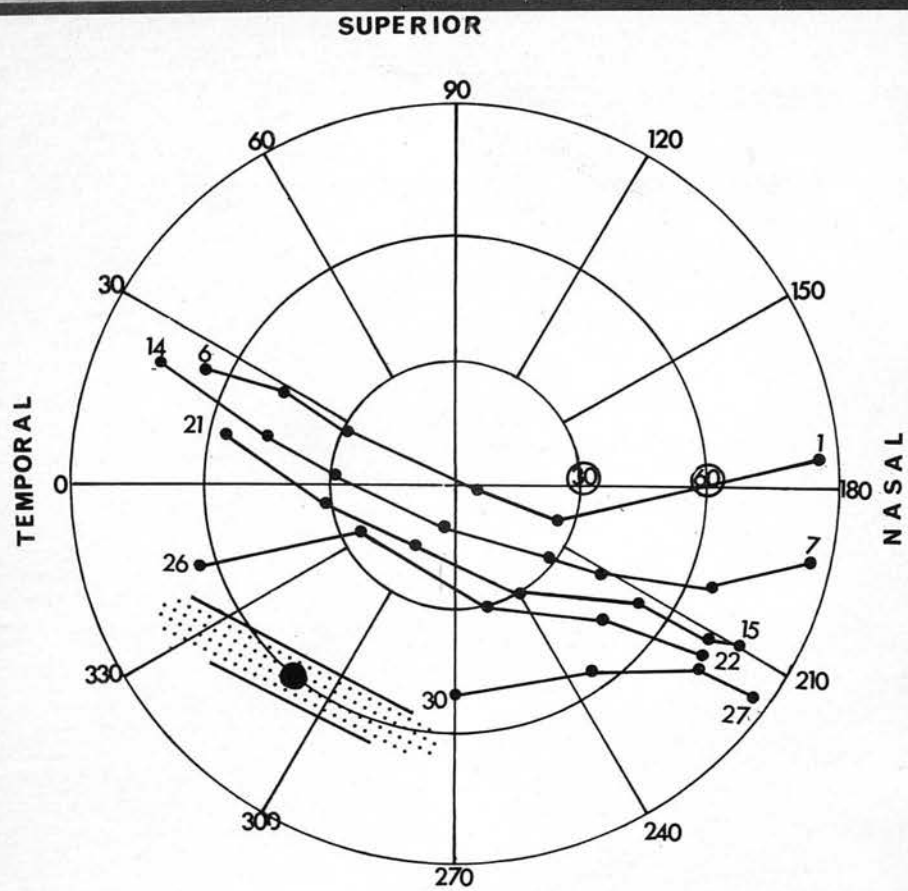
R_3

RABBIT, DORSAL VIEW, RIGHT SUPERIOR COLLICULUS.

Fig. 34

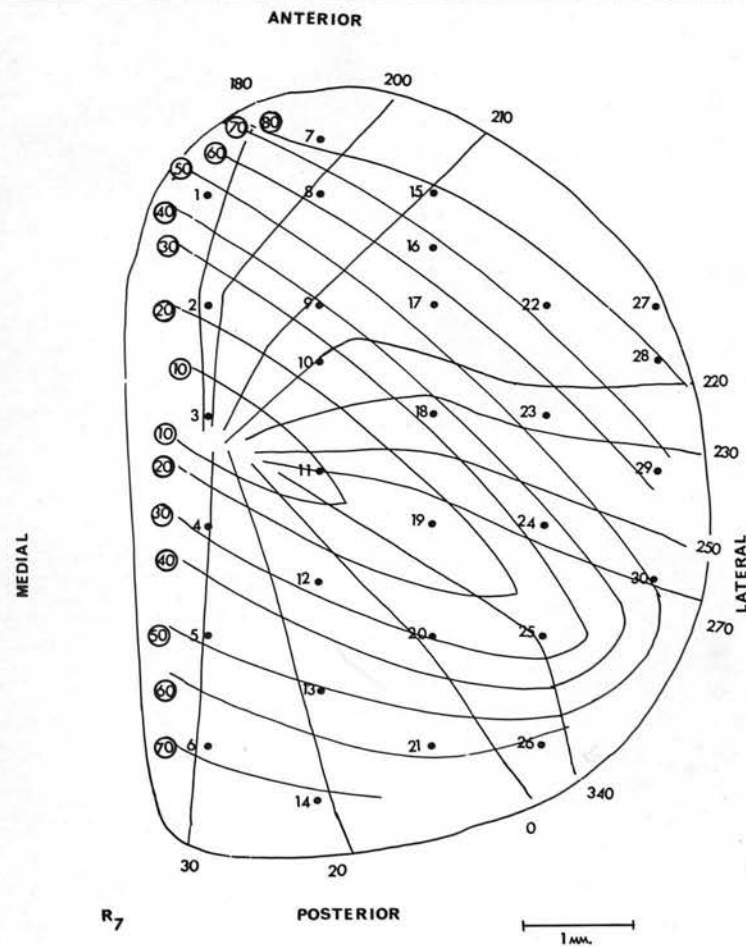
Experiment R₇. Projection of left visual field on dorsal surface of right colliculus.

Projection of myelinated band on visual field indicated by stipple, black disc denotes optic nerve head.



R₇

RABBIT. VISUAL FIELD OF LEFT EYE.



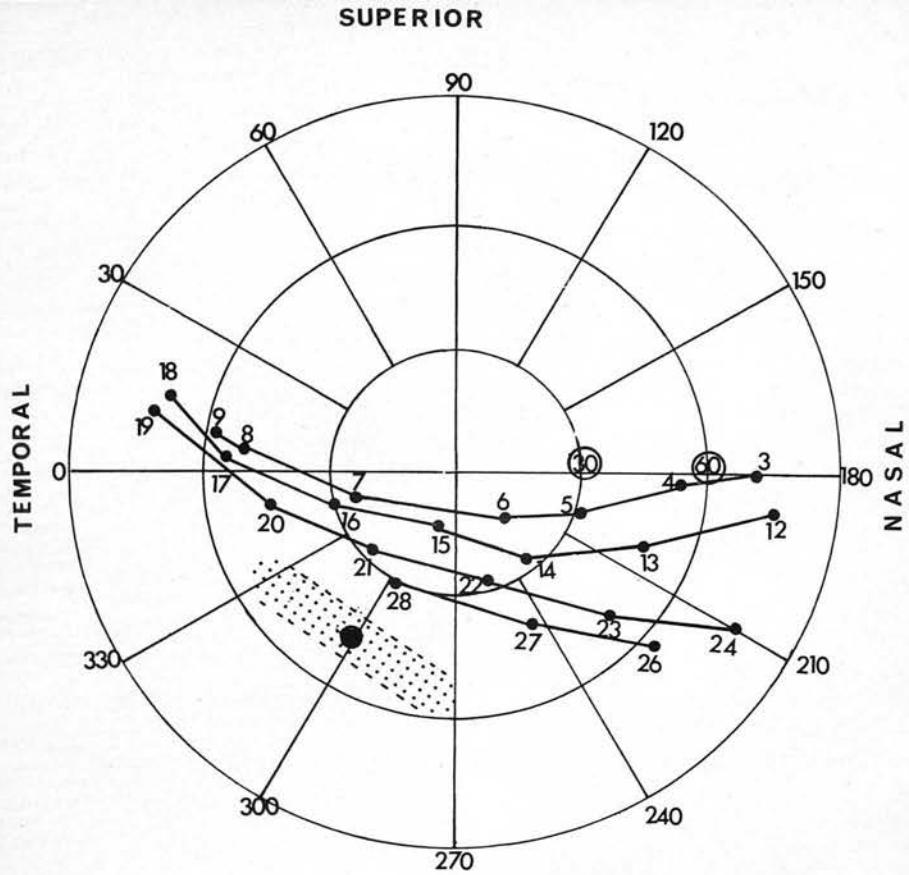
R₇

RABBIT. DORSAL VIEW, RIGHT SUPERIOR COLLICULUS.

Fig. 35

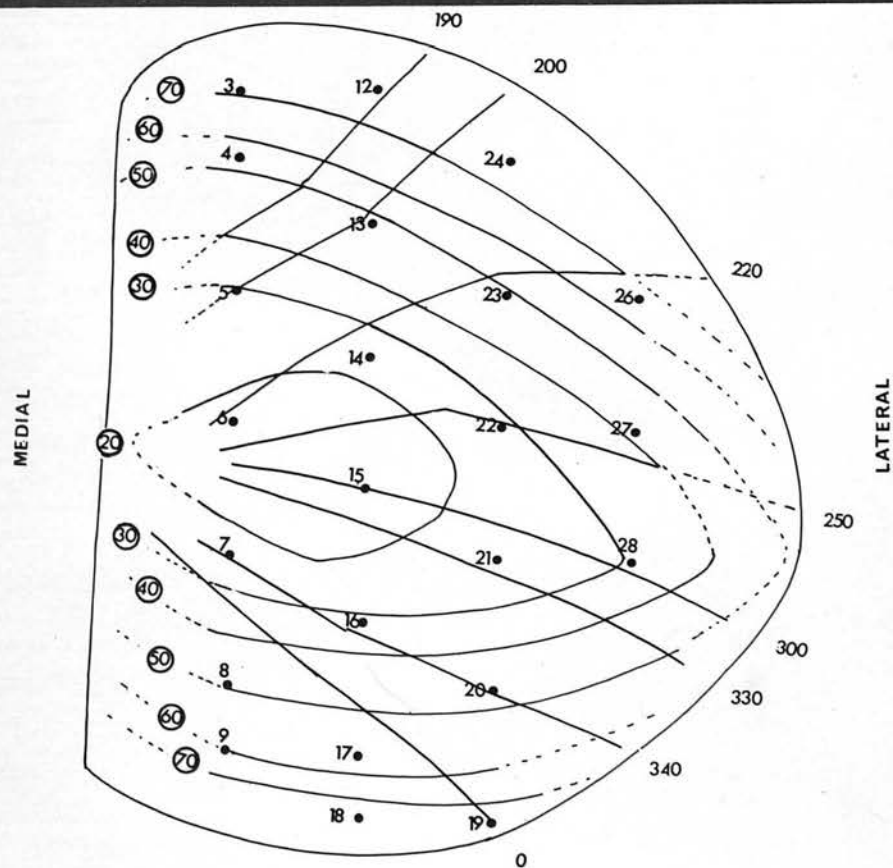
Experiment R₁₇. Projection of left visual field on
dorsal surface of right colliculus.

Projection of myelinated band on visual field
indicated by stipple, black disc denotes optic nerve head.



R₁₇

RABBIT. VISUAL FIELD OF LEFT EYE.



R₁₇

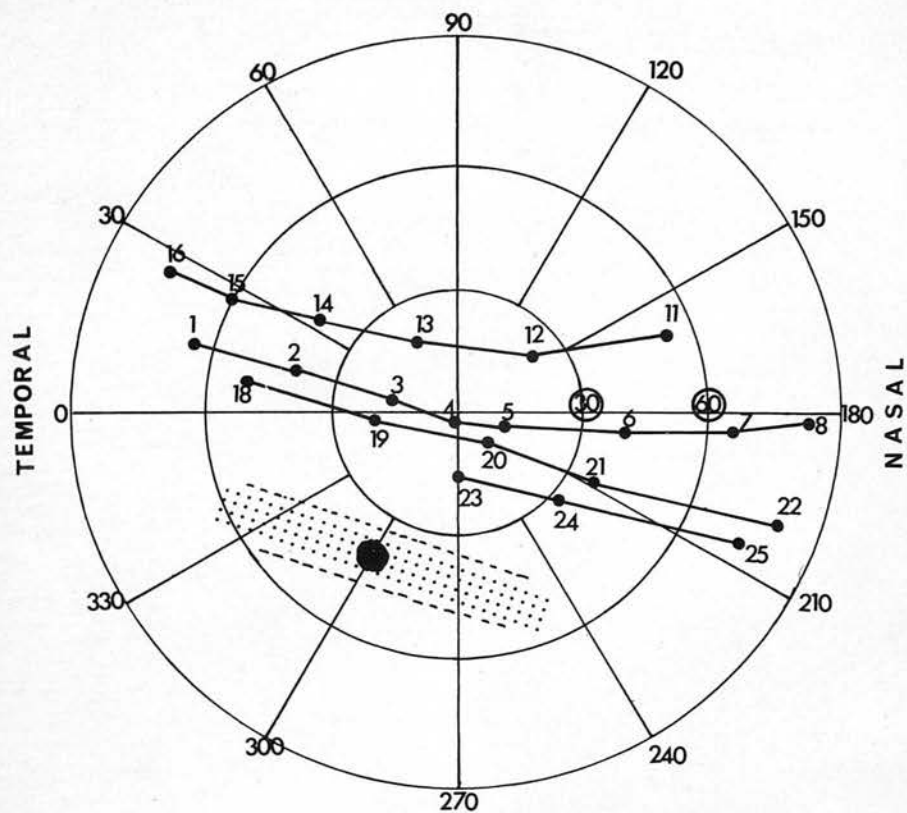
RABBIT. DORSAL VIEW. RIGHT SUPERIOR COLLICULUS

Fig. 36

Experiment R₁₈. Projection of left visual field on dorsal surface of right colliculus.

Projection of myelinated band on visual field indicated by stipple, black disc denotes optic nerve head.

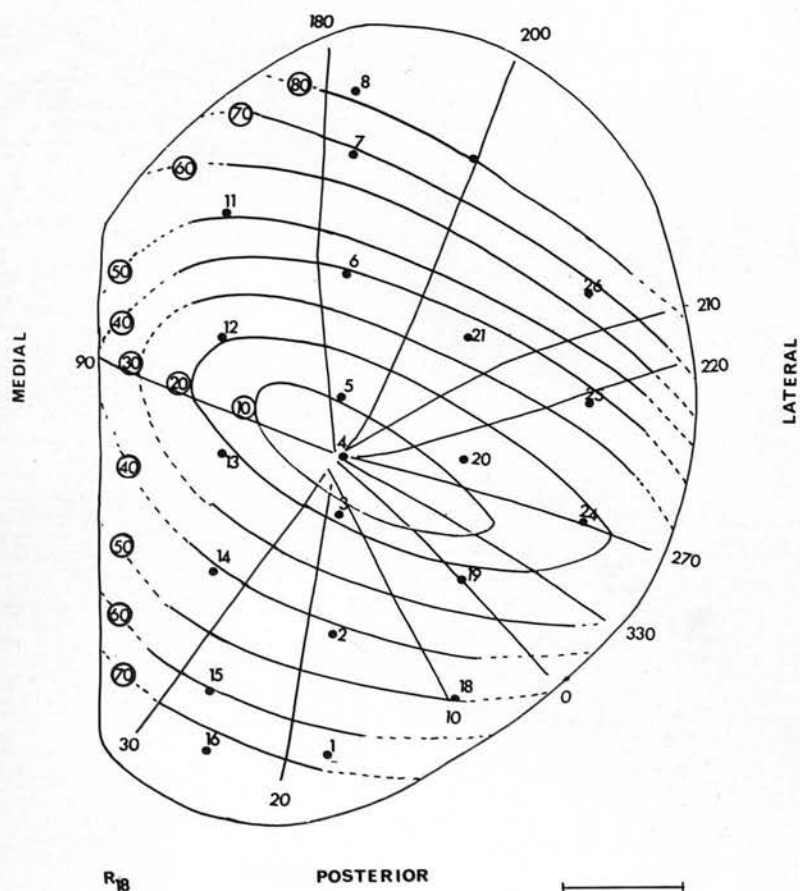
SUPERIOR



R₁₈

RABBIT. VISUAL FIELD OF LEFT EYE.

ANTERIOR



R₁₈

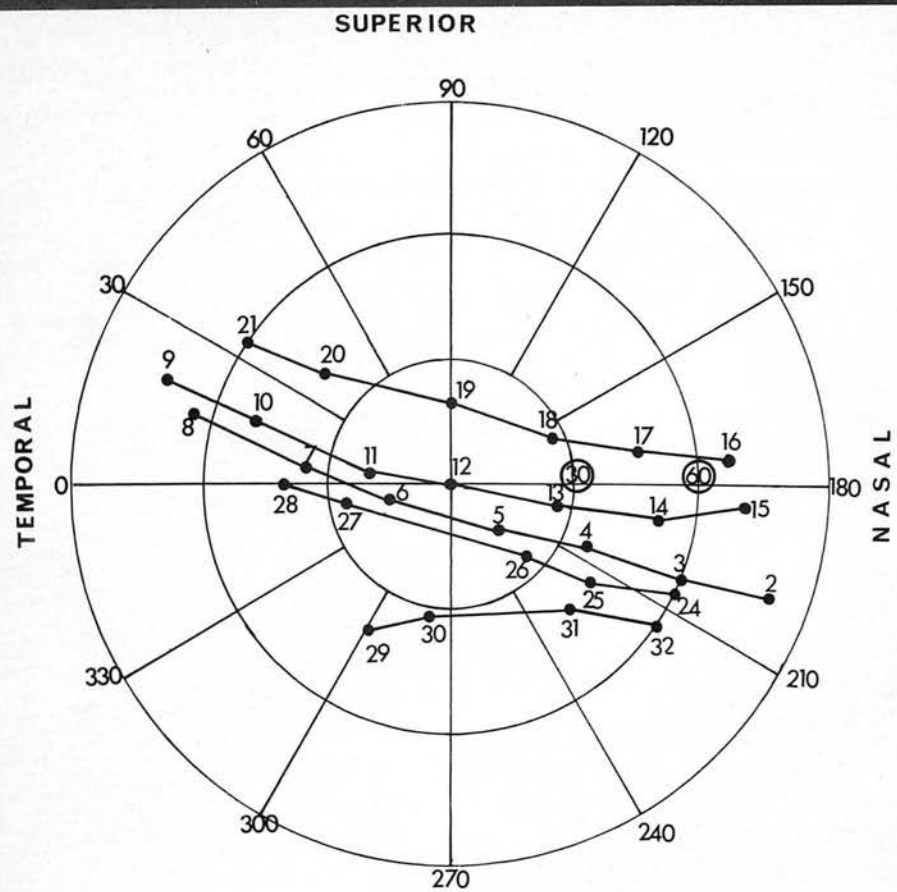
POSTERIOR

1 mm.

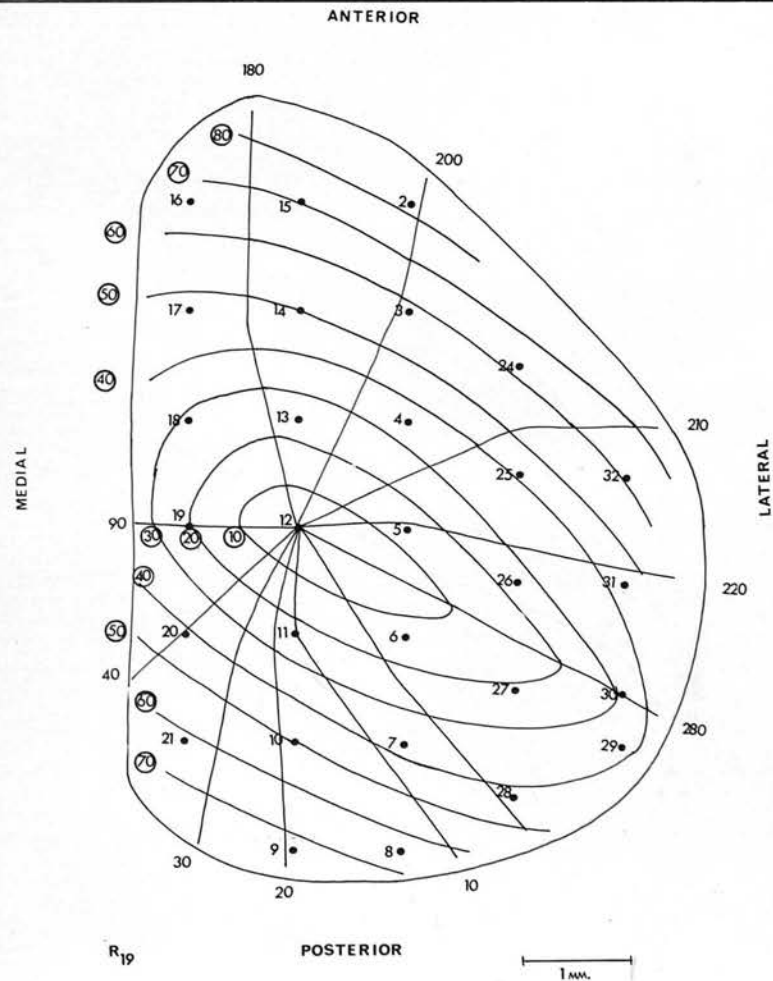
RABBIT. DORSAL VIEW RIGHT SUPERIOR COLLICULUS

Fig. 37

Experiment R₁₉. Projection of left visual field on
dorsal surface of right colliculus.



RABBIT. VISUAL FIELD OF LEFT EYE.



RABBIT. DORSAL VIEW. RIGHT SUPERIOR COLLICULUS.

Fig. 38

Variation of magnification factor with retinal eccentricity, for visual field points along the vertical meridian. Composite results from Experiments R₃, 7, 17, 18, 19.

Fig. 39

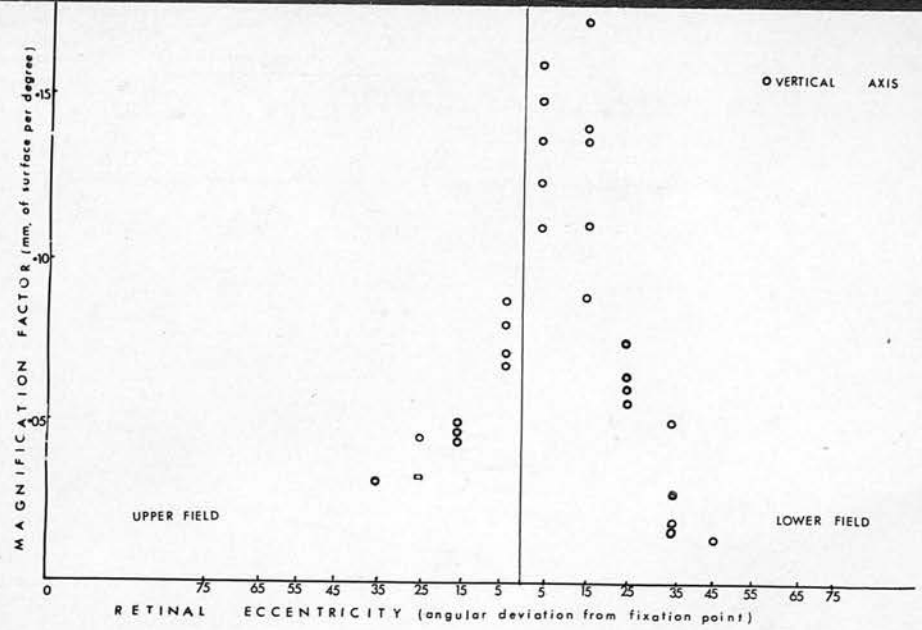
Variation of magnification factor with retinal eccentricity, for visual field points along horizontal meridian. Composite results from Experiments R₃, 7, 17, 18, 19.

Fig. 40

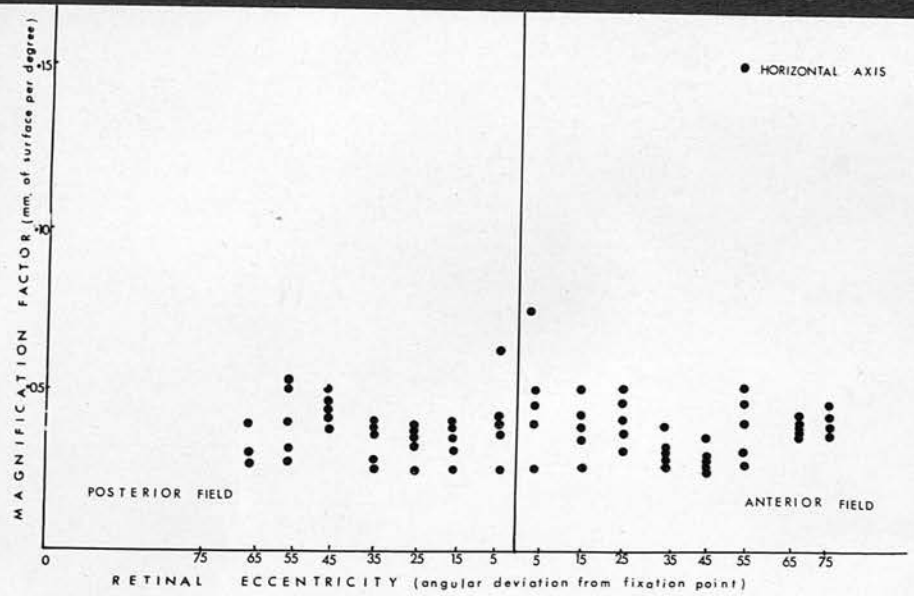
Retinal ganglion cell concentration 'contours'.

Horizontal strip of retina, 6 mm. wide, containing optic nerve head, myelinated nerve fibre band, and 'visual streak'.

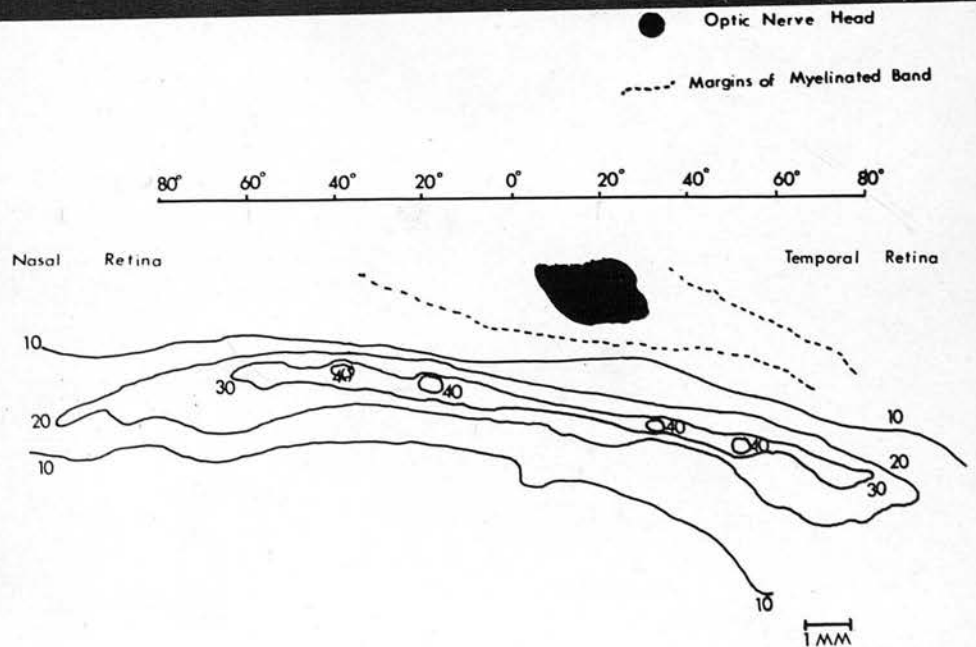
The figures at the end of the 'contour' lines indicate the ganglion cell concentrations, in a strip of retina of unit length, i.e. 300 μ , in sections 10 μ thick.



R3, 7, 17, 18, 19.



R3, 7, 17, 18, 19.

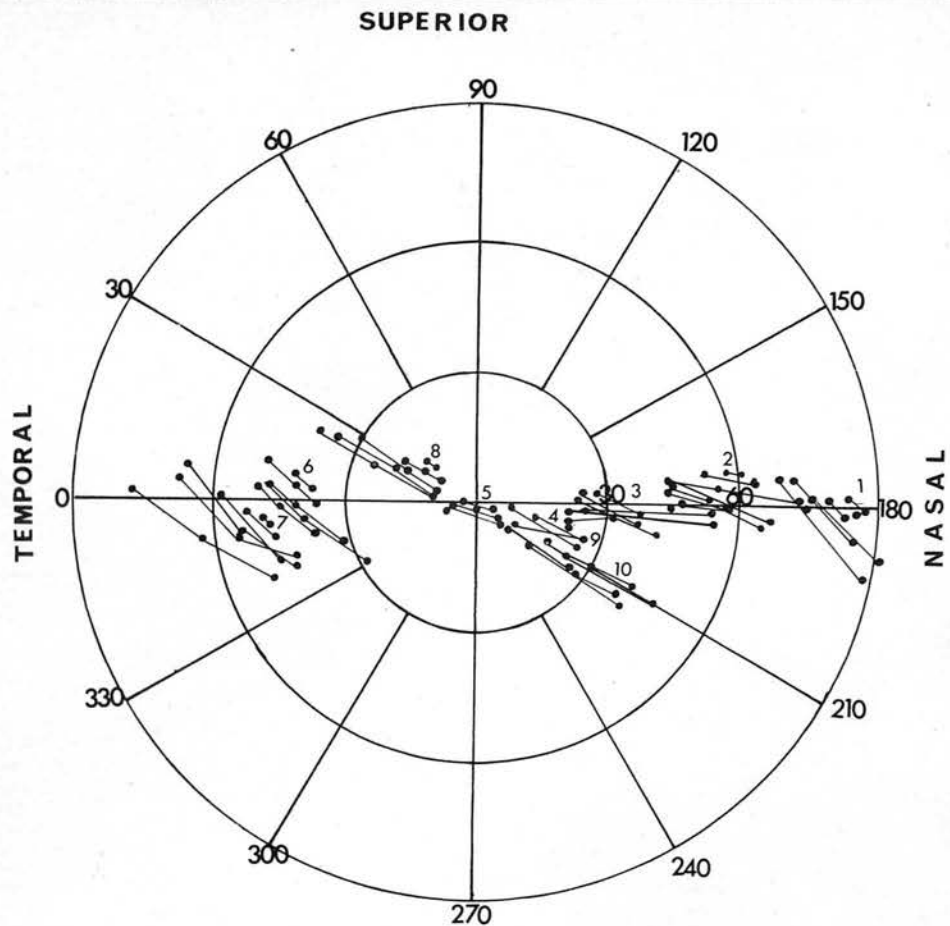


RETINAL GANGLION CELL CONCENTRATIONS.

Fig. 41

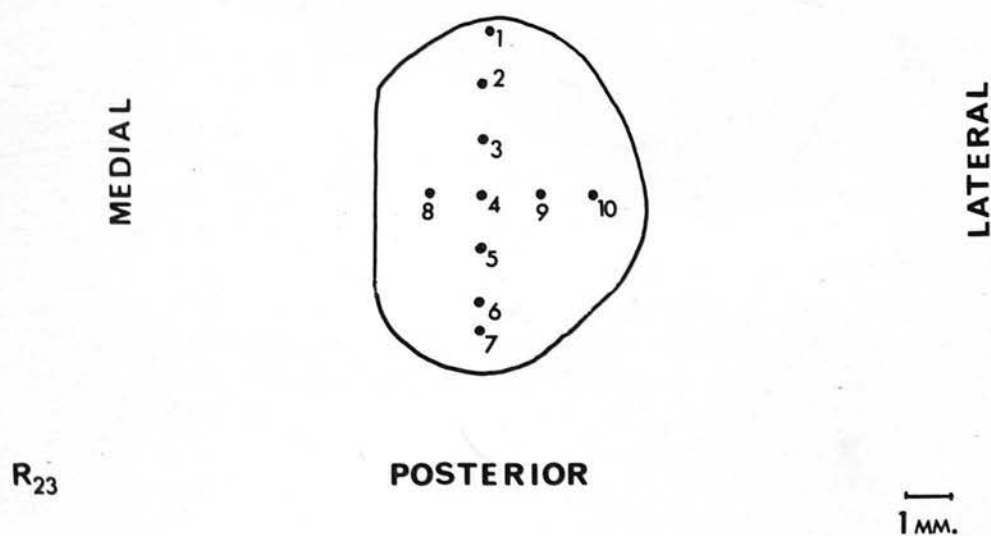
Changes in size and position of the receptive fields with progressive penetration of superior colliculus in 500 μ steps.

The long axes of the elliptical receptive fields are indicated by lines.



R₂₃

RABBIT. VISUAL FIELD OF LEFT EYE.



R₂₃

RABBIT. DORSAL VIEW, RIGHT SUPERIOR COLLICULUS.

IV. DISCUSSION

The primary object of this study has been the investigation of the projection of the visual field on to the surface of the lateral geniculate nucleus of the cat. This task demands the ability to define the position of a point in visual space, and, since the connections between the retina and the geniculate nucleus are anatomically determined, to determine the projection of the point in space on the retina. Since, however, the eye of the cat is movable within the orbit, it then becomes necessary to establish a fixed relationship between the system of co-ordinates used to define position in visual space and the retina in terms of the retinal landmarks. The problem then resolves into one of choosing a suitable system of co-ordinates and of establishing the retinal landmarks in a fixed position in relation to a point of reference of the chosen co-ordinates.

1. Visual Field Co-ordinates.

Although several systems of co-ordinates are available, none of them satisfy the ideal requirements. In these experiments a perimetric system, with spherical polar co-ordinates and a horizontal

axis passing through its reference point and center, has been used, the choice being dictated by several considerations:-

- a. Every direction in the visual field is defined by a unique co-ordinate that can be easily determined during the course of an experiment, and the angular difference subtended at the eye by any two points in the field can be readily calculated from the coordinates of each point.
- b. For the investigation of the peripheral fields, the perimeter offers unique advantages over the tangent screen systems, for the stimulus-eye distance, and consequently stimulus size, shape and illumination intensity, are maintained constant over the entire extent of the field.
- c. The use of a perimeter with a built-in light source permits of a great variety of stimuli of varying size and intensity to be used with considerable ease.
- d. The use of a perimeter system for studies on experimental animals makes the results so derived more easily comparable with those derived from clinical neurology, where perimetric methods have been

are conventionally accepted and extensively used.

Yet, however, the use of a perimetric method entails two chief drawbacks:-

- a. The accuracy of localization within 5° of the reference point is limited by the convergence of the meridians; for this purpose, tangent screens permit of greater accuracy.
- b. If lengths in the visual field are to be expressed in terms of the angles subtended at the eye, then the co-ordinate system should ideally be such that the length of a unit of the co-ordinate system is constant over the surface of the reference sphere, and equal in every direction; such a system would yield a grid, equally spaced between its co-ordinates, a condition which does not hold for perimeter co-ordinates.

This feature is of particular disadvantage in a study such as this where the prime experimental object has been to demonstrate quantitatively the differential distortion of particular parts of the visual field. An ideal system of co-ordinates would have permitted of direct comparison of unit

areas of visual field and retinal surface, with the distorted areas on the surface of projection. The use of a perimeter system hence entails the need for a more indirect method of estimation of this distortion, e.g. Magnification Factor which is a measure of linear distortion along a chosen plane.

2. The Position of the Eye.

The second aspect of the problem is the determination of the axis and plane of reference for the eye which is to be maintained in a fixed relationship to the co-ordinates of the perimeter. For this purpose, it has been assumed that the center of the area centralis retinae and the nodal point of the eye define the direction of the fixation axis of the eye, the projection of this axis on the visual field constituting the fixation point of the eye. In human perimetry the fixation plane is a horizontal one, containing the two fixation axes when the head is vertical and the eyes look straight ahead. The eyes are said to be in their primary position when the visual axes are in the fixation plane and directed upon a common fixation point at infinite distance, for in this position corresponding retinal points are similarly orientated. Since there is no method of determining

directly the disposition of the axis and plane of fixation of the eye in its primary position in an unanaesthetized cat, it has been assumed that the plane is a horizontal one, and the eye has been fixed in this position by locating it at the center of the perimeter and moving it such that the fixation axis becomes coincident with the axis of reference of the perimeter. anatomically fixed, it

Bishop, Kozak and Vakkur 1962 argue that the positions of the eyes in Man during anaesthesia, or after complete ophthalmoplegia "is usually not far from the anatomical position of rest, and usually approximates within a few degrees the primary position of the eyes". On this basis they determine the positions of the fixation axis and of the projection of the "blind axis" in the completely paralysed cat. Under these conditions, they observe that the fixation axis is inclined upwards and very slightly divergent with respect to the Horsley-Clarke horizontal and sagittal planes; the mean divergence for each eye - i.e. declination being 2.6° and the mean inclination 12.6° . Should the primary position of the eye of the normal cat be that of the completely paralysed eye, it would mean that in this series of experiments the eye has been rotated down through 12.6° , about an axis passing through the area centralis; thus the field center

and vertical meridian if displaced upwards through 12.6° would correspond with the extent of the vertical meridian as determined by Bishop et al. Such an upward displacement would only increase the vertical extent of the upper field and diminish the extent of the lower field by 12.6° relative to the true horizontal plane, for, since the retino-geniculate connections are anatomically fixed, it could not alter the relative proportions of the surface of the geniculate devoted to the representation of the upper and lower retinal halves. The experimental results of this study suggest that in the vertical meridian the field extends for about 50° above fixation point and for about 80° below it. If then, as Bishop et al suggest, the area centralis projects in life to 12.6° above the horizontal, it would ascribe to the cat a vertical extent of field about 62° above the horizontal and 68° below it, a feature difficult to reconcile with the cat's essentially terrestrial habits.

Retinal ganglion cell degenerations following optic tract section in kittens, Ganser 1882, suggest that the visual field of each eye is split into halves by a vertical axis passing through the fixation point. Bishop, Kozak and Vakkur 1962 confirm this view from their own study of retinal degeneration and study of receptive fields of

geniculate neurones of both sides in the region of the vertical meridian, and conclude that "in the normal unrestrained animal the medial borders of the homonymous hemi-fields are presumably parallel and vertical when the eyes are in their primary position, thus co-inciding with the zero meridian".

In this series the micro-electrode studies have been carried out on the left L.G.N., consequently the right eye was aligned with its fixation axis coincident with that of the reference axis of the perimeter, and the projection of the right hemi-field of the left eye on lamina A_1 of the left geniculate studied by rotating the left eye to such a position that its fixation point too was projected on the point of reference of the perimeter, hence coincident with that of the right eye. In such a position, it is presumed that the medial margins of the hemi-fields of each eye would be vertical and coincident if no rolling of either eye had occurred. Under these conditions the binocular extents of the homonymous hemi-fields should overlap each other exactly, hence a binocularly activated unit should respond to stimulation of either eye from a single stimulus position; so, too, adjacent units in laminae A and A_1 , or A_1 and B, should have receptive fields in very close proximity to one another, and all the localizations

obtained from the left geniculate should be strictly confined to the right hemi-field, with a distinct delineation of its medial border, i.e. the vertical meridian.

These requirements establish criteria of the reliability of the experimental method, for in all the successful experiments of this series these demands were satisfied to within a few degrees of error. Thus in Experiment C₃₄ the upper vertical meridian, i.e. 0° - 90° , was clearly established, and a more medial position of the electrode recorded from units in the mirror image of the I^{RY} projection rather than from the adjacent part of the left hemi-field; similarly, exploration of the antero-inferior part of the L.G.N. yielded localizations strictly confined to the lower quadrant of the right hemi-field.

3. Retino-topic Projection on the L.G.N.

The only histological study of the projection of the visual field of the cat on the L.G.N. is that of Overbosch 1927. He has, however, described the projection in terms of the retinal quadrants obtained by vertical and horizontal lines through the optic disc. Since, however, the vertical axis dividing the field into right and left

hemi-fields is one passing through the area centralis, which lies well temporal to the disc, Overbosch's "temporal" quadrants include a vertical strip of the true nasal retina; consequently his geniculate projection maps consist of projections from all four of his retinal quadrants. Hubel 1960, Hubel and Wiesel 1961, studying the receptive fields of single units in the L.G.N., provided evidence that the central visual fields were represented to a disproportionately large extent on the medial aspect of the nucleus, and that the lower field was represented anteriorly. Bishop, Kozak, Levick and Vakkur 1962, recognizing the functional significance of the area centralis, studied the projection of the true hemi-retina on the L.G.N. Choosing a system of spherical polar co-ordinates whose polar axis passes through the nodal point of the eye, at right angles to the presumed fixation plane, they define position in the visual field in terms of two angles - "azimuth", i.e. the angle to the right or left of the zero meridian measured from the fixation plane, and "elevation" which is the angle above or below the fixation plane - and their projection maps of the visual hemi-field have been prepared by superimposing a grid of iso-azimuth lines (meridians) and iso-elevation lines (parallels) on laminar maps of the L.G.N. in the Horsley-Clarke

coronal and parasagittal planes. They, too, find the upper field quadrant projecting posteriorly on the nucleus, with the lower field anterior and the peripheral field lateral on the nucleus. Their projection maps, however, reveal that the upper field has been explored only to an extent corresponding to 5° of elevation above the fixation plane and the lower field to 40° below the fixation plane, while their exploration of the peripheral field has been up to a limiting value of 30° azimuth. This limited extent of the field mapped would not have revealed to these workers the disproportionate representation of the upper and lower field quadrants, the disposition of the "projection lines" in the posterior region of the nucleus, or the projection on the medial interlaminar nucleus.

The results of this study confirm the observations of Bishop et al and extend the study of the projection of the field on to a great extent of the surface of lamina A. Although the differences in the systems of co-ordinates used, and of the planes of orientation of the fixation axes, make direct comparison of the results difficult, the essential similarity between the projection maps is evident. Thus the different retinal areas have corresponding areas of projection, and the spacings of their iso-elevation lines on the

parasagittal section of the nucleus and of their iso-azimuth lines on the coronal sections resemble very closely the projection of the meridians and semi-circles of equiangular deviation obtained in this study. Their two estimates of the magnification factor, corresponding to 10° deviation from fixation point, 0.13 mm./degree, and to 30° deviation, 0.025 mm./degree, are in perfect agreement with the results of this series.

The most significant feature of the projection map of the surface of lamina A is the disparity between the areas devoted to the representation of the upper and lower field quadrants, a fact made more relevant by the fact that the lower visual quadrants correspond to the tapetal retina. Bishop et al have not studied the projection of the upper field quadrants, nor is Apter's 1945 study of the visual field projection on the surface of the superior colliculus sufficiently precise to permit of confirmation of this observation. A more accurate study of the projection of the fields on the superior colliculus would be of interest, either to confirm the observation that the tapetal and non-tapetal retinae receive disproportionate areas of representation, else to establish that the collicular pattern of projection is fundamentally different from that of the geniculo-

striate system, emphasizing thereby some functional difference.

The retinal ganglion cell concentration studies relate well with the spacing of the projection lines which represent the degree of eccentricity from fixation point, but do not reflect the disparity of the surface areas devoted to the representation of the upper and lower field quadrants.

Little is as yet known of functional differences between ganglion cells and of the basis of their distribution in the retina, so too of the proportion and basis of distribution of the optic tract fibers and of the nature of these fibers in different parts of a particular lamina in the L.G.N. Similarly, knowledge of the total cell count of the geniculate, with the proportion of this assigned to each lamina and of the proportion of cells with exclusively non visual afferents, is lacking, hence little more than speculation about the nature of ganglion cell-geniculate neurone connections can be made.

Since the retina devotes equal numbers of its ganglion cells to upper and lower retinal quadrants (Figure 29), while the geniculate assigns fewer of its neurones to the upper field than to its lower, it implies that each "upper field ganglion cell"

makes connection with a smaller number of "upper field geniculate neurones" than does a "lower field ganglion cell" should the total number of visually activated geniculate neurones exceed the total number of ganglion cells. This hypothesis implies a divergence of neural paths, an increase in the number of channels through which visual information passes centrally at the geniculate level; conversely, if the total number of geniculate neurones is smaller than the number of ganglion cells, each "upper field geniculate neurone" would connect with more "upper field ganglion cells" than do the "lower field geniculate neurones". Under these circumstances upper field geniculate neurones would have receptive fields proportionately larger than those of the lower field geniculate neurones, implying thus a diminished acuity for the upper field in comparison with the lower. The presence of the tapetum in the upper retina is perhaps indicative of the functional importance of the lower field, for the tapetum, being in effect a post retinal mirror, serves to increase the light sensitivity of the upper retina - Granit 1943, Weale 1953, Dodt and Walther 1958, Campbell 1961. Such intra-ocular scattering of light by the tapetum would tend to diminish the acuity discrimination of the tapetal retina; hence the relatively smaller convergence

of the "tapetal ganglion cells" on to the "lower field geniculate neurones" than of the "non tapetal ganglion cells" on to the "upper field geniculate neurones" may represent a compensatory adaptation, giving the cat enhanced sensitivity and acuity in this part of its visual field.

4. The Medial Interlaminar Nucleus.

Little attention has been paid to the nucleus interlaminaris medialis since its description by Thuma 1928. Hayhow 1958 confirms Thuma's observations that the nucleus had ipsilateral and contra-lateral retinal connections and that it contained a mixed population of cells - large, small and giant sized - resembling those in the pars-dorsalis. Nothing is known of its efferent connections, although a second cortical visual area, Talbot 1942, and a suprasylvian visual area, Marshall, Talbot and Ades 1943, Clare and Bishop 1954, Buser and Borenstein 1956, 1957, Vastola 1961, with an organized pattern of retino-topic projection have been described. Buser and Borenstein believed the suprasylvian response to be mediated by a projection from parts of the posterior thalamic nuclei, medial to the L.G.N., whereas Marshall, Talbot and Ades, and Vastola believed that the

extra-striate responses in the suprasylvian gyrus showed characteristics of a primary projection pathway from the L.G.N. Thus they persisted after ablation of the cortices and collicular bound pathways and isolation of the ipsilateral L.G.N. from the pretectal and medial thalamic nuclei, and were abolished by anodal depolarization of the ipsilateral L.G.N., or after retrograde degeneration of the L.G.N. consequent to ablation of the striate cortex. The medial interlaminar nucleus might well satisfy these requirements.

The functional significance of these secondary cortical areas remains as much in doubt; Talbot 1942 could find no characteristic difference between the responses in this area and those from the I^{ry} cortical area under a variety of experimental conditions.

There have, however, been suggestions that some efferents of the L.G.N. do not terminate in the striate cortex, and hence do not contribute to visual sensation. Minkowski 1920 believed the cells of the lamina magnocellularis to be concerned with cortically mediated eye movements, believing that in the cat the visual and oculogyric functions of the retino-tectal projections

of the lower acorticate vertebrates were in the act of being given over to the new retino-cortical paths through the L.G.N. Walls 1953 suggests that of the two visual cortices only one is sensory, with the other having, possibly, motor functions and hence being physiologically more comparable with the primates' Area 18. He writes "one only has to suppose that the rabbit and cat have never hit upon the primates' clever trick of combining a complete occipital oculo-motor center with a sensory center, in the same patch of cortex. Thus instead of operating fixative, field holding, and related reflexes by means of cells situated right in Area 17 (as does the primate) the lower form has to have a separate visuo-motor cortex containing a built-in motor map of the visual field, and the retina has to supply to this cortex duplicate spatial information of which the animal is never conscious. It has not been shown that the upcoming fibers entering Area II arise from L.G.N. cells, but the chances seem heavy that they do".

5. Lamination and Projection Lines in the L.G.N.

The characteristic feature of the histophysiology of the cat L.G.N. is its lamination, for even though lamination is a common structural feature in

the anatomy of the retina, superior colliculus and visual cortex, the significance of the laminar pattern of the L.G.N. is entirely different. Elsewhere the cells at different levels are different in their functions and the neat ordering of their bodies into layers makes room for intervening synaptic beds in which specific activities are carried on. In the L.G.N., however, "there are no obvious rewards for lamination, the fibrous interlaminae are axon mats, not synaptic beds, for there is no instance of intercommunication from lamina to lamina or across interlaminae in the L.G.N. of any mammal", Walls 1953.

In the cat on each of its three layers is represented a visual hemi-field, and when the homonymous hemi-fields of the two eyes overlap each other exactly, a single point in the visual field is represented along a line passing through all three layers. Bishop, Kozak, Levick and Vakkur 1962 refer to this as a projection line and envisage it as "consisting of hundreds of neurones arranged along bundles of optic tract axons which have originated from corresponding small areas in the two retinae", and Walls 1953 writes more fancifully of a "tooth-pick in a club-sandwich".

The histological evidence, Tello 1904, Taboada 1927, O'Leary 1940, confirms the view that the large

anterior division of the optic tract enters the L.G.N. chiefly through its narrow ventral hilus; from here the terminal bundles run transversely across the laminae taking up after the manner of radii the curves presented by the anterior semi-spherical region of the nucleus. In each lamina the fiber divides to form a spindle shaped terminal arborization, the long axis of each spindle being at right angles to the surface of each lamina and the successive spindles in the laminae being arranged in a line across the thickness of each lamina. The distribution of optic tract axons to the posterior region of the nucleus is slightly different, for here the posterior division of the optic tract forms a nearly vertical fibrous plate applied closely to the posterior surface of the vertical curl of the nucleus, with the terminal tract afferents passing anteriorly to penetrate the laminae B, A₁ and A. Thus the projection lines in this region of the nucleus would be determined by the disposition of the tract fibers in an antero-posterior plane. Direct experimental proof of this would necessitate the passage of an electrode through the laminae in the plane of the afferents, i.e. antero-posteriorly, an experimental condition near impossible to fulfil; yet localizations obtained from two vertical penetrations, one

immediately posterior to the other, through the vertical extent of the curl adduce evidence that the projection lines are orientated antero-posteriorly.

"The structural arrangement of projection lines across the cellular laminae enables a given small retinal area to retain a precise topographical arrangement in the L.G.N., while at the same time retinal fibers could be sorted out to terminate at different stations along the length of the projection line, possibly in terms of qualities of information. The dense terminal arborizations of the optic tract fibers and the cross linking between adjacent fibrillary glomeruli, clearly provide the basis for complex data processing in the L.G.N.", Bishop et al 1962. This concept of a functional subdivision in a column of cells is not a new one, for it has interesting parallels with those described by Hubel and Wiesel 1962 in the visual cortex of the cat, and in the somato-sensory cortex of the cat by Mountcastle 1957; here too, the sensory area concerned can be subdivided, on the basis of responses to natural stimuli, into regions which are roughly columnar in shape, the columnar organization being superimposed upon a spatial pattern of topographical representation.

With reference to the L.G.N., this concept is in effect a restatement of Walls' 1953 "cartological theory of geniculate lamination". Walls conceived the laminae of the geniculate as a pile of maps of the visual field, related "to each other as are three maps of the same country, one of which is geodetic, a second climatological, and the third agricultural. Just as three maps are required to keep such kinds of information apart and intelligible, so also a mammal with highly differentiated vision requires a multiplicity of genicular maps if the cortex is to be able to make full use of the classified information the retina sends it".

Thus for the cat, Walls would envisage the visual information from the right hemi-field to be contained on the three laminar maps of the left L.G.N., the nasal hemi-retina of the right eye channelling the information into the two contralateral laminae A and B, while the temporal hemi-retina of the left eye transmits its information to the single ipsilateral lamina A_1 . In effect then, visual information from a single point in the field undergoes a process of "sorting out" in the corresponding points of temporal and nasal retinae of the two eyes, and the information so processed transmitted to the geniculate by at least three "diageniculate" pathways; since the terminal

tract afferents are distributed in the nucleus in a radial arrangement, each diageniculate pathway could separate from its fellow and terminate in its appropriate lamina. The projection line would then represent the common path of all the diageniculate paths activated from a single point in the visual field. Walls cites the evidence from comparative anatomy in substantiation of his theory that the lamination principle does not relate to binocularity, diurnality, nocturnality, colour vision nor to duplex versus simplex retinae, per se, but that what are separated in different laminae are different diageniculate paths for "in any mammal with completely discriminative vision, there will be certain diageniculate path types which could safely be allowed to be closely approximated where they go through the geniculate station, for the whole raison d'etre of the station was its provision of opportunity for multiplication or overlapping of paths and this could never have been permitted unless it were true that there were some path types that can be allowed to be short-circuited without this making impossible a subsequent unscrambling of their messages at cortical level".

Most of the knowledge hitherto gained about the L.G.N. of the cat may be interpreted in these terms. Thus the characteristic histological

differences between the cellular patterns in the laminae A and A_1 on the one hand and B on the other, Thuma 1928, O'Leary 1940, Hayhow 1958, have already been reviewed.

Hubel and Wiesel 1961 found electrophysiological evidence of differentiation of the receptive fields in units of lamina B from those of A and A_1 ; thus they find "B" responses to be more sluggish and these units tended to have larger receptive fields, a view confirmed by the observations of Bishop et al 1962. The experimental results of this study provide further evidence, for B units were found to have lower light thresholds, larger receptive fields, to have a greater tendency to behave as continuous "off center" units and to display a "dark adaptation" like phenomenon, in contrast to units in laminae A and A_1 . The units in these layers resemble each other in all respects - receptive field size, shape, threshold, and relative proportions of center "on" and "off" types. In addition to a segregation of incompatible geniculate pathways into different laminae, A and A_1 display also evidence of an intralaminar segregation of paths which are perhaps less incompatible, one with the other, for in these laminae "on" and "off" center units are differentially distributed.

Thus it would seem that visual information

from a single stimulus position in the field serves as the input to a column of geniculate cells situated along the projection line, the data being processed at different levels along its extent before this functional unit, together with its adjacent columns, could serve as the input to a cortical column, whereas Hubel and Wiesel 1962 suggest the more complex analyses of pattern can occur.

The laminar segregation of units with small central receptive fields and prominent peripheral inhibitory effects in laminae A and A_1 away from units in B which have demonstrably larger fields, greater light sensitivity, diminished peripheral inhibitory effects and an increased proportion of continuous "off" effects, seem very suggestive of a differentiation of acuity and sensitivity mechanisms. It is conceivable that the units of A and A_1 are concerned with the accurate detection of the edges of a retinal image, for the provision of units with small central fields and antagonistic peripheral surrounds which respond with short bursts of activity would be an effective mechanism for increasing the contrast of image outlines. Units on each side of an illuminated edge would then be more readily activated than those that lie within the center of an illuminated area; thus edge contrast would be enhanced, although infor-

mation relating to the actual level of illumination of the image or of its background would be lacking. In contrast to this, the functional activity of B units with their large receptive fields, paucity of peripheral inhibitory effects, and increased sensitivity to levels of background illumination, would be well suited to signal continuously the relative levels of illumination of image and background with but poor resolution of image edge. The intralaminar segregation of center "on" and center "off" units in laminae A and A₁ may serve yet another method of contrast enhancement. Since visual information is transmitted along nerves by modulating the impulse frequency, continuously firing "off" center units would have to be used for signalling decreases in stimulus intensity, but where there is a resting discharge this is rarely so high that there is as much room for a decrease of frequency as there is for an increase, and further, when the pulse frequency is increased the time resolution improves, whereas if it is decreased it gets worse. If then increases and decreases of light are equally significant, and since the transmission system is thus essentially asymmetric, inverting the signal would combat the difficulty. In these terms the center "on" units would then transmit a "positive picture", whereas

the retino-topically equivalent group of center "off" units a "negative picture", thus effectively increasing between them the delineation of the edge.

The thickness of the laminae suggests that several other diageniculate paths, mediating other and more complex modalities of vision, are likely, but as yet the detection of these poses formidable experimental problems.

In terms of Walls' Theory it is tempting to speculate that, since "the whole extent of the visual" field is spread over the surface of the lamina, its varying thickness in different parts is indicative in some way of the number of diageniculate paths which reach that region, for the greater thickness would permit of relatively more complex "processing". The projection maps of this study establish clearly the relationship of the lower field and tapetal retina to the thickened anterior region of the L.G.N. where all three of its constituent layers are significantly thickened. It is also significant that, though the surface areas of a lamina devoted to representation of unit areas of the visual field diminish markedly with retinal eccentricity, the thicknesses of the laminae do not show a comparable variation, for each lamina remains of almost uniform thickness in the part of it representing the tapetal retina.

This feature is most evident in layer B, for here the part corresponding to the tapetal retina is uniformly thicker than the corresponding regions of A and A_1 , whereas the extent of B corresponding to the non-tapetal retina and upper visual field is greatly reduced and uniformly thinner than the comparable extents of A and A_1 . This structural relationship between B and the tapetum is matched by the behaviour of its units with their lower thresholds, larger fields, and sensitivity to levels of background illumination. The functional significance of the lower field, served by the tapetal retina, hence seems characterized by lamina B serving its sensitivity mechanisms, whereas the increased thickness of layers A and A_1 represent enhancement of its acuity discrimination.

The distribution of the lamina magnocellularis within the pars-dorsalis shows a similar relationship to the tapetal retina, for it is in the "tapetal" part of the L.G.N. that these giant cells are found in their largest numbers, and only here do they show sufficient aggregation as to constitute a distinct lamina. Granit 1962 suggests that since the projections from each L.G.N. to the cortex deliver "hemi-field images", the neurophysiological mechanisms for fusion of these hemi-field images at the border line are based on the activity of

these magnocellular binocularly activated units. The distribution of these magnocellular elements in relation to the retinal topography on the L.G.N. makes it unlikely that the process of "fusion" of the hemi-field images occurs along their vertical medial borders, for these cells have a specific distribution along the projection of a horizontal axis. Under these circumstances, it is more likely that instead of "fusion" along the vertical border, the laminae magnocellularis of each L.G.N. enable the two hemi-fields to be aligned, one against the other, such that their central projections maintain between the two cortices a continuity of "images" across the visual field along a horizontal axis.

Since the lamina A_1 , from a temporal hemi-retina, matches perfectly the lamina A with its nasal hemi-retinal connections, it is only lamina B, also from a nasal hemi-retina, that lacks its counterpart; thus it would seem that in the cat's retina there must be some diageniculate path types leading away from the nasal hemi-retina which are entirely lacking in the temporal. Thus, in spite of the striking co-relation of the tapetum with the structure and function of lamina B, the true functional significance of B must be even more complex, for the tapetum extends into the temporal

as well as nasal hemi-retinae and hence the lamina B must in addition contain the projections of yet other diageniculate paths, derived exclusively from the nasal hemi-retina.

Walls 1953 discusses these naso-temporal differences and suggests that in the evolution of frontality of the visual axes the nasal retinae retain their archaic decussating connections to the contralateral cerebral centers and pathways, while the relatively "newer" temporal pathways now involved in binocular vision gain ipsilateral connections to the cerebral centers. Walls suggests that in the course of this transition the temporal retinae lose some of their ancestral properties which are as yet retained by their nasal fellows. He suggests in point that prior to the advent of binocularity, perception of oculo-centric direction would have depended on cortical directional signs characterized by complete fixity, but that with two retinae contributing to a binocular image, by way of nasal and temporal elements, fixation of the two eyes about a single field point, by twelve eye muscles without error, would become impossible; hence the "implication is strong that it was the temporal hemi-retina which had to make most or all of the concessions to make itself an acceptable mate for the nasal area it co-operates with".

Walls cites several other examples of observed naso-temporal differences, derived chiefly from clinical neurology, but until the retina yields confirmatory evidence of structural and functional differences between its nasal and temporal halves, this problem must remain largely speculative.

6. Non-Visual Connections of the L.G.N.

The unique characteristics of lamina B make it concerned with several other problems of geniculate function. Thus the locus of termination of the radiation fibers that arise from its cells is uncertain. O'Leary 1940 observed some fibers arising from cells in this lamina re-entering the optic tract, but was uncertain of their final terminations. Bishop and Clare 1955 were of opinion that these fibers projected to the lateral nucleus of the thalamus, although degeneration of the cells in lamina B after extirpation of the striate cortex, Polyak 1927, suggests that some radiation fibers or their collateral branches project directly to the cortex. Non-visual sources of geniculate activation clearly exist; Hernandez-Peon, Scherrer and Velasco 1956 observed modification of geniculate responses during simultaneous stimulation of the brain stem cone, and Hubel 1960 observed modifications of geniculate cell firing patterns in

unrestrained cats when the animals passed from a sleeping to a "wakeful" state, while Jung 1958 noted in the cat's visual cortex a similar dependence on the state of its activity. Niemer and Jiminez-Castellanos 1950, and Jasper, Ajmone-Marsan and Stoll 1952 have adduced evidence of cortico-fugal projections to restricted parts of the L.G.N. Widen and Ajmone-Marsan 1961 elicited cortico-fugal effects on the L.G.N. by stimulating a small area on either side of the border line between cortical visual areas I and II. They observed that a cortical conditioning stimulus could facilitate or inhibit a geniculate spike response produced by an optic tract or photic test stimulus, whereas conversely an optic tract or photic conditioning stimulus could similarly facilitate or inhibit an L.G.D. spike elicited by a cortical test stimulus. Differentiating between the effects of antidromic stimulation of the optic radiation and orthodromic stimulation of the specific cortico-fugal fibers, they believe that their experimental evidence indicates that a large proportion of the observed effects were due to the orthodromic activation of the cortico-fugal pathways. They conclude that their findings provide some evidence for the existence of specific, probably extra-reticular, cortico-fugal mechanisms, but give no information about

the site within the L.G.N. of this interaction.

These observations of Widen and Marsan run parallel with the evidence that has accumulated in recent years which emphasizes the role of the brain stem reticular formation, not only in its influences on motor descending pathways but also in its control of sensory mechanisms by exerting their influence at sub-cortical levels where most of the interactions with the sensory input from the periphery take place.

This evidence promotes the view that the L.G.N. can no longer be thought of as a practically independent relay station, meant merely for the transmission and spatial reorganization of the visual signals, for it does seem likely that the L.G.N. "sorts out" the signals to permit some, or all, of them to undergo varying extents of interaction with cortical and brain stem influences prior to final recoding of the visual signals before they are finally "unscrambled" at a cortical level.

7. Rabbit - The Retino-topic Projection on the Colliculus.

The experimental results obtained in this study reveal the pattern of representation of the visual field on the superior colliculus. These

results agree well with those obtained by earlier workers; thus Pavlow 1900, Loepp 1912, Minkowski 1920, and Jefferson 1940, using degeneration techniques, were of opinion that no ipsilateral retinal afferents reached the colliculus. Brouwer 1923, Brouwer and Zeeman 1927, and Overbosch 1927, making small retinal lesions, traced the degenerating fibers to the colliculus, deducing thereby the pattern of projection of the visual field, while Hamdi 1953, Hamdi and Whitteridge 1953 used electrophysiological methods to demonstrate the projection of the horizontal and vertical meridians on the collicular surface. More indirect evidence is provided by the work of Thompson, Woolsey and Talbot 1950 who determined the projection of the visual field on the rabbit's cortex. Their work attributes to the rabbit an extensive field of monocular vision about a horizontal plane, the vertical extent of the field represented being extremely limited, confined to about 15° above and 20° below the horizontal meridian. Although they could find no clear evidence of an area of enhanced resolution in the vicinity of the fixation axis, they mention the likelihood of a second retinal area of enhanced resolution for nearward vision.

The results of this study confirm the views

of Talbot, Woolsey and Thompson 1950 that the monocular field of vision of the rabbit is an extensive horizontal band of limited width; in addition, there is probably, in the vicinity of the true fixation axis, a small retinal area wherein the resolution seems minimally enhanced; so too, in addition to the nasal retinal area for enhanced nearward vision, there may be in the temporal retina a corresponding retinal area of slightly increased resolution for anterior nasal vision.

Preliminary studies of the projection of the visual field on the L.G.N. of the rabbit - Choudhury and Whitteridge - unpublished, reveal a pattern markedly similar to that seen on the colliculus - the field represented here too is a narrow band with evidence of areas of increased resolution in regions of the L.G.N. corresponding to the anterior and posterior ends of the "band of vision".

The change in shape of receptive fields with increasing depth in the colliculus finds confirmation in the work of Schafer 1962. Schafer, recording from single units, finds that a flickering light source is an effective stimulus for collicular units situated in its superficial layers, whereas units in the deeper layers could be activated only by moving stimuli showing directional specificity. This is in accord with the findings of this study,

for the receptive fields of surface units are small, whereas the deeper units have narrow and elongated elliptical fields orientated along a specific axis, the latter units being most effectively activated by a narrow bar shaped patch of light, or movement of a small source along the axis of the receptive field.

The role of the superior colliculus in vision must of necessity be greatly dependent upon the extent to which a geniculo-striate system has developed. In the lower vertebrates the optic tectum is the main station for visual projections, whereas in monkeys what remains after degeneration of the L.G.N. is a primitive kind of light discrimination, Kluver 1942, and in Man no signs of sub-cortical optokinetic movements are seen in cases of blindness from cortical lesions, though persistence of optokinetic nystagmus has been claimed in coma in the new-born and in cases of "extreme idiocy", Whitteridge 1960. Thus it seems very likely that the direct visual connections to the superior colliculus become smaller and less important as the cortico-collicular connections from Area 19 become relatively more important, Whitteridge 1960 after Petersen and Henneman 1948.

The role of the superior colliculus in the control of eye movements has been a source of

of considerable interest, and the extensive literature resulting from experimental ablation and stimulation studies has been reviewed, Apter 1946, Hamdi 1953, Whitteridge 1960.

In the cat, Apter 1945 demonstrated the projection of the visual field on the collicular surface, and in 1946 showed that after strychnine-ization of a point on one collicular surface, diffuse illumination of either eye caused conjugate deviation of both eyes towards the corresponding area of the visual field. This would lead to the conclusion that each colliculus has efferent connections which regulate in a systematic manner the activity of the oculo-motor nuclei, though it does not in itself indicate the source, or sources, of the information by which these movements are controlled.

Very little is known about the control of eye movements in the rabbit or of the functional significance of its superior colliculus. The laterally placed eyes give the rabbit an extensive field of monocular vision; Thompson, Woolsey and Talbot 1950 claim a limited binocular field of 20° , claiming also that the eyes can be medially rotated through about 10° to increase the anterior field of binocular overlap. The results of this investigation reveal a very precise projection of the

visual field on the superior colliculus, more elaborate perhaps than essential for the mediation of this limited range of eye movement. The high degree of resolution across the narrow width of the visual field makes it seem more likely that the colliculus is concerned to a greater extent with the integration of the vestibulo-ocular reflexes, thus enabling the rabbit to keep effectively within this narrow band of enhanced acuity all objects of interest to it, despite considerable variations in the position of its head in space.

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